

DOCTORAL THESIS

Modelling Approaches to Primate Conservation

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Modelling Approaches to Orangutan and Chimpanzee Conservation

by

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Abstract

The future survival of the orangutan is extremely uncertain; as hunting and deforestation continue to exert pressure on surviving populations, new threats such as climate change and potential disease transmission are emerging that may exacerbate an already critical situation. The potential impacts of these threats were investigated in this thesis using modelling approaches, to provide insights that will be valuable for planning effective conservation strategies. Anthropogenic factors were identified as important determinants of the current range of the orangutan, while resting time also appeared to be a key constraint on orangutan distribution patterns. This may be related to a greater reliance on fallback foods in degraded habitats, leading to increased digestion times and hence excessively high resting time demands. In the future, anthropogenic effects were predicted to continue to have an important influence on orangutans, particularly as they were found to be extremely sensitive to habitat degradation across the whole of their current range. In contrast, climate change was not predicted to be a major threat to the orangutan, although large increases in rainfall could lead to considerable range reductions.

Modelling disease spread revealed that although potential superspreaders were identified in the orangutan population, the orangutan social system was extremely robust against disease transmission, irrespective of the model or disease parameters used. As such, vaccinations were not predicted to be useful. However, modelling disease transmission within a chimpanzee community suggested that orangutans living in a more gregarious manner, for example, in rehabilitation centres, may be highly susceptible to disease spread. Overall, although climate change and disease transmission were not predicted to be strong pressures, the extreme vulnerability of the orangutan to further habitat degradation across its range suggests that the development of even relatively minor threats could have important ramifications for the survival of the species.

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1. Introduction

1.1 The conservation of great apes

All of the great ape species are endangered, facing a range of threats to their future survival (IUCN 2013). These threats, such as habitat loss and hunting, are likely to intensify in the future as the human population continues to grow, and demand increases for resources from tropical rainforests (Wright 2005). The emergence and development of new threats such as climate change and the potential spread of infectious disease could exacerbate an already critical situation (Chapman et al. 2006, Suhud and Saleh 2007). The ability of conservation initiatives to tackle these challenges successfully depends on a detailed scientific understanding of both the species and the problems that they face. Chimpanzees (*Pan spp.*) and gorillas (*Gorilla spp.*) have been studied relatively extensively for the past 50 years, with a number of groups habituated for both research and ecotourism (Woodford et al. 2002, Goldsmith 2005, Robbins et al. 2005, Pusey et al. 2007). In contrast, there have been fewer studies of orangutans (*Pongo spp.*), perhaps linked to the elusive behaviour of the species and the difficult field

conditions of many of the field sites as well as their more distant evolutionary relationship to humans (van Schaik 2004). As such, there exists a much larger body of literature on the behaviour and conservation of the African apes than their Asian relative; a search on Web of Knowledge, for example, using the phrase “chimpanzee conservation” returns 1,213 papers, “gorilla conservation” 1,045 while “orangutan conservation” only 457. In order to conserve the orangutan effectively into the future, a greater emphasis needs to be placed on orangutan research without which conservation action cannot succeed.

1.2 The conservation of the orangutan

The orangutan is on the brink of extinction, surviving in fragmented patches of rainforest on the islands of Borneo and Sumatra (Delgado and van Schaik 2000). In the coming decades it is imperative that conservation measures are designed that respond effectively to the threats currently facing the orangutan such as widespread deforestation and hunting (Sugardjito 1995, Meijaard and Wich 2007). However, the new threats that are emerging such as climate change and disease transmission mean that it will also be necessary to adopt a more proactive approach to conservation, predicting and responding to threats before they fully materialise. Modelling approaches provide a useful method through which these threats can be predicted and their potential future impact assessed. In this thesis, both the current and future distribution of the orangutan will be explored and potential disease transmission investigated using modelling approaches, to provide valuable new insights into the conservation of the species.

One of the major prerequisites to planning conservation initiatives is knowledge of a species distribution (Sugardjito 1995). The distribution of the orangutan is thought to be

limited by geographical barriers and low quality forest at high altitudes (Rijksen and Meijaard 1999, Husson et al. 2009). Over the last century the range of the orangutan has undergone a substantial reduction in size and this has largely been attributed to hunting pressures and deforestation (Rijksen and Meijaard 1999). However, behavioural factors can also restrict the distribution of a species; if more time needs to be spent performing the behaviours that are essential for survival than is available in the day, a species will be unable to survive. This could occur, for example, if the quality of the available food is so low that there is not enough time for an animal to meet its nutritional requirements (Dunbar 2002). Determining these behavioural limitations will improve current understanding of the relationship between the orangutan and its habitat. This will also provide indications of the suitability of different habitats for orangutans and their ability to survive in increasingly modified landscapes. This is an area that has not yet been investigated in relation to the orangutan but may have important implications for their survival into the future.

Issues that may increase in importance in the future include climate change and disease transmission. Climate change may lead to habitat shifts and novel conditions across the range of the orangutan. In extreme cases this could render the remaining orangutan strongholds uninhabitable. The effect that climate change is likely to have on the orangutan has not yet been investigated beyond speculative suggestions (Suhud and Saleh 2007) or analyses of subsections of their overall range (Gregory et al. 2012), and so it is important to investigate this in more detail to provide broader insights into the future distribution of the species. Increases in deforestation and in the human population densities of Borneo and Sumatra that can be expected to occur in the future will lead to orangutans and humans living in increasingly close proximity to one another. This is likely to lead to an increase in the risk of inter-specific disease transmission. The threat

of disease will also increase as ecotourism becomes more popular and the number of tourism sites and visitors rises. Disease transmission is therefore likely to become an increasing problem for the orangutan in the future, yet the study of disease spread between orangutans has been relatively neglected to date. The role of individuals in spreading disease, the efficacy of vaccinations as a preventative measure and the susceptibility of the orangutan to the spread of different types of diseases, for example, are areas that have not previously been explored. An investigation of these aspects of disease transmission could provide valuable information for conservation, such as highlighting the types of diseases that will be of greatest conservation concern and identifying action that could be taken to prevent widespread epidemics.

Habitat fragmentation may exacerbate the threat of disease by forcing orangutans to live at higher densities in the remaining patches of suitable land. Orangutans in rehabilitation centres, whose release may ultimately have a major impact on the size of the wild population, already live at much higher densities. Increased population densities may lead to changes in social system and potentially increased gregariousness, which is likely to have an important effect on the risk of disease transmission. This potential difference in disease risk can be investigated by comparing predicted disease dynamics for the orangutan with those from a closely related species, the chimpanzee. As the chimpanzee has a similar but more gregarious social system, it is a good model for a more social orangutan, and can provide a valuable indication of the disease risk faced by orangutan populations living at higher densities than wild individuals. Assessing disease risk in the chimpanzee is also crucial for our understanding of both current and future threats to this species.

There are clearly considerable gaps in our knowledge regarding the conservation of the orangutan, particularly concerning distribution patterns and potential disease

transmission. The aim of this thesis is to investigate these aspects of orangutan conservation. This will produce new insights that will contribute to our understanding of the conservation of these species. This thesis is composed of six chapters. The current chapter presents an introduction to the orangutan and its conservation, followed by an overview of current knowledge regarding distribution patterns and disease transmission. A broad discussion of the questions that will be addressed and the methodologies that will be employed in this thesis is also included. The chapter concludes with the statement of research questions. The second and third chapters address questions relating to the distribution of the orangutan, both now and in the future. The second chapter uses a time budget model to estimate the current distribution of the orangutan and identify the behavioural factors that restrict this distribution. The level of social flexibility is also investigated. Social flexibility (i.e. the ability to survive under a range of group sizes and therefore alter this according to changing conditions) can be viewed as a means through which a species can cope with and adapt to future change. The level of social flexibility predicted for the orangutan is investigated across the entire range of the species. The third chapter uses the time budget model to predict the effect of climate change and human population growth on the ability of orangutans to survive within their current range. The fourth and fifth chapters focus on disease dynamics among orangutans and chimpanzees, employing social network analysis and agent based modelling. The fourth chapter assesses the role of both individuals and the overall population structure in the spread of disease, and the efficacy of vaccinations on disease dynamics. The fifth chapter presents the results of simulations of the spread of disease within both species; this provides insights into the ease with which different types of diseases are transmitted. The sixth and final chapter includes a summary of the major findings and provides a discussion of broader implications.

1.3 The orangutan

1.3.1 Orangutan biogeography

During the Early and Middle Pleistocene, orangutans were distributed across South-east Asia, including large parts of the mainland such as Vietnam, Cambodia, Thailand, Laos, southern China and India (Rijksen and Meijaard 1999, Harrison et al. 2006, Louys et al. 2007). In addition, orangutans were widely distributed across Borneo (Harrison 2000), Sumatra (Hooijer 1949) and Java (Rijksen and Meijaard 1999). However, the orangutan's range has declined dramatically and is currently restricted to small populations on Borneo and Sumatra.

The distribution of the orangutans on mainland Asia contracted during the Pleistocene and by the Holocene, orangutans were no longer present in mainland Asia (Jablonski 1998). This decline has been attributed to both climatic and anthropogenic factors. From the Early to the Late Pleistocene, tropical and subtropical zones shifted southwards and eastwards while seasonality increased, which may have pushed the orangutans closer to the less seasonal equatorial regions (Jablonski 1998). Orangutans are specialised to a largely frugivorous diet, and this, combined with their exceptionally slow life histories, may have prevented them from adapting to the increased seasonality; fruit became so irregular that individuals may have been unable to maintain their body weight, while food shortages may have delayed female age at first reproduction and increased inter-birth intervals (Jablonski et al. 2000). Orangutans were then unable to recolonise their past range once the tropical conditions returned to mainland Asia, as elevated sea levels meant that dispersal across the Sunda shelf was no longer possible (Jablonski et al. 2000). However, Delgado and van Schaik (2000) argue that human factors are also likely to have played an important role in this decline and failure to recolonise. Mass

extinctions of megafauna occurred in every continent with the exception of Antarctica during the Pleistocene (Louys et al. 2007). These extinctions happened at different times in different places, usually following the arrival of humans, suggesting that global climate change was not responsible (van Schaik 2004). The incomplete fossil record means that it is difficult to entirely support or refute this argument, but the current lack of evidence for severe hunting pressures across mainland Asia suggest that while human impacts may have contributed, climatic changes are likely to have been largely responsible for the extirpation of the orangutan from mainland Asia (Jablonski 1998, Louys 2008).

The impact of humans, however, does appear to have had a strong influence on the distribution of the orangutans within Borneo and Sumatra. The first groups of human hunter-gatherers are likely to have arrived on these islands around 40,000 years ago, with the first cultivators arriving approximately 6,000 years ago (Rautner et al. 2005). In Sumatra in particular, the early human colonisations proved to have a negative impact on orangutan populations (Rijksen and Meijaard 1999). Cave remains indicate that these early groups hunted the orangutan, and it has been suggested that the absence of the orangutan from many areas of apparently suitable habitat in both Borneo and Sumatra is the result of past extirpations as a result of hunting by the indigenous people (Sugardjito 1995, Rijksen and Meijaard 1999, Harrison 2000). At the Niah caves in Sarawak, for example, orangutan subfossils are found in abundance, often with clear indications of human consumption such as bone charring (Harrison 1996). The orangutan does not now occur within hundreds of miles of this site (Medway 1977, Wich et al. 2008). Hunting has continued up to the present and so orangutans have not been able to recolonise these areas (Rijksen and Meijaard 1999).

Human pressures have increased in the last 200 years with the intensification of deforestation; indeed, the overall orangutan population size is thought to have declined by more than 95% in this time (Goossens et al. 2006). Encounter rates by early nineteenth century explorers were around six times higher than current rates, suggesting that orangutans occurred at much higher densities in the recent past (Meijaard et al. 2010b). Orangutans have specific habitat requirements and so deforestation has been extremely damaging. Orangutan habitat includes peat-swamp forests, freshwater swamp and alluvial forests in valleys, and the lowland and hill forests dominated by dipterocarp trees (Rijksen and Meijaard 1999, Knott and Kahlenberg 2007, Husson et al. 2009). Orangutans have also been found at lower densities in heath forest, limestone-karst forest, palm stands and mangrove forests (Husson et al. 2009). Most of Borneo and Sumatra were once covered with these habitat types and so orangutans were widely distributed, but the combination of hunting pressures and deforestation have reduced this distribution to the small pockets that remain (Husson et al. 2009).

1.3.2 Life history and social organisation

There are two species of orangutan, the Sumatran species (*Pongo abelii*) and the Bornean species (*P. pygmaeus*), which comprises three subspecies (*P.p. wurmbii*, *P.p. pygmaeus* and *P.p. morio*). Orangutans have an extremely slow life history, intermediate between humans and the African great apes. It has been suggested that Bornean orangutans have faster life histories than the Sumatran species, as a result of higher mortality on this island; life history theory suggests that higher mortality will lead to a faster paced life history (Stearns et al. 2000, Wich et al. 2009). In the wild, both males and females can live to around 50 years of age (Harvey et al. 1987). Females do not tend to reproduce for the first time until around 15 years old. Gestation lasts around 260

days, and females generally have one infant per birth (Harvey et al. 1987). Female orangutans have extremely long interbirth intervals of around nine years, longer than any of the African great apes, and longer on Sumatra than Borneo. This is likely to be a result of the lower fruit availability in South-east Asia, which prevents orangutans from having more than one infant at a time (Wich et al. 2004). It is still uncertain why infants remain with their mothers for such an extended period, but this may be related to the acquisition of foraging or social skills, or the need for protection from predators such as clouded leopards or from conspecifics (van Adrichem et al. 2006). These slow life histories place orangutans at a high risk of extinction as it takes many years for populations to recover from the loss of individuals, for example from hunting, deforestation or disease (Marshall et al. 2009). Slow life history was found to be significantly associated with high extinction risk in declining carnivores and primates (Purvis et al. 2000) while slow reproductive rate was associated with a population decline following logging in primates (Cowlshaw et al. 2009).

Male orangutan life histories are characterised by an extremely unusual feature, bimaturism, whereby two forms of mature males exist: flanged and unflanged males. Unflanged males appear to remain in a state of ‘arrested’ development (Utami et al. 2002), in which they retain many of the features associated with adolescent individuals, such as short hair, a flat chest and hard rims on the side of the face (Kingsley 1982). Males have been observed to stay in this unflanged stage for up to 20 years (Utami et al. 2002). Flanged males on the other hand are the socially dominant form; these are larger individuals, with characteristic large, flanged cheek pads. These males also develop a muscular throat pouch, longer thicker hair and grow considerably in size (Kingsley 1982).

Two main explanations have been suggested for the arrested development of unflanged males. One suggestion is that the presence of socially dominant flanged males prevents the development of secondary sexual characteristics in unflanged males by causing them to experience high stress levels which inhibit development. It has been shown in zoos, for example, that adolescent males housed with flanged males will not develop flanges until a later stage than those housed as lone males (Kingsley 1982). However, a study of stress levels in a number of orangutans at different levels of development showed that only adolescents that were already developing secondary sexual characteristics had elevated stress levels. This indicates that chronic stress is not arresting the development of unflanged males (Maggioncalda et al. 2002). An alternative explanation is that the unflanged stage represents an alternative reproductive strategy for males that would not achieve dominant status were they to continue developing. Unflanged males are largely tolerated within the home ranges of flanged males, and can occasionally achieve copulations, often by force (Utami et al. 2002). In contrast, flanged males are relatively intolerant of other flanged males within their territories (Utami Atmoko et al. 2009a). Therefore, remaining unflanged can be a beneficial reproductive strategy, at least until the resident flanged male dies or moves territory.

Orangutans have an unusual mating system in that females have large home ranges that overlap considerably. Flanged males can have home ranges three to five times the size of those of females, and will therefore overlap with a number of females (Utami Atmoko et al. 2009a). There is intense competition between males for females, but flanged males are the preferred mating partners (Utami Atmoko et al. 2009b). These dominant flanged males will form consortships with females, and attempt to prevent unflanged males from mating with them (Utami et al. 2002). However, as females are

widely dispersed in both space and time it is difficult for flanged males to maintain control over the females and prevent unflanged males from forcing occasional matings (Schurmann and van Hooff 1986).

This dispersed social structure means that orangutan densities are often low, and large areas of forest are required to support relatively few individuals (Husson et al. 2009, Marshall et al. 2009). This clearly exacerbates the effects of habitat loss on this species; for example, it has been estimated that fragments of rainforest smaller than 500-1000km² cannot support a genetically healthy population of Bornean orangutans (Marshall et al. 2009). Low population density was also found to be significantly associated with high extinction risk in declining carnivores and primates (Purvis et al. 2000).

Orangutans have traditionally been viewed as solitary individuals, who socialise only for brief consortships or with dependent offspring (Mitra Setia et al. 2009). Although orangutans do spend the majority of their time alone (Galdikas 1985a), it has been increasingly recognised that they are not as asocial as previously believed. At Tanjung Puting, for example, orangutans were observed to spend 19% of their time in groups (Galdikas 1985a), while at Ketambe orangutans formed groups in 30% of observations (Rijksen 1978). Importantly, these early studies showed that these groupings were not restricted to adult males and females associating in a mating context (Mackinnon 1974, Galdikas 1985a). More recent studies have shown that Sumatran orangutans may even form loose communities with neighbouring individuals. These communities or ‘clusters’ comprise potentially related females that preferentially associate with one another (Singleton and van Schaik 2002, van Noordwijk et al. 2012). Thus, the orangutan social system may be more complex than previously assumed and may be similar to the fission-fusion system found in chimpanzees (van Schaik 1999).

Orangutans may gain a number of benefits from grouping. A widely accepted advantage to forming groups is to gain protection from predators (Wrangham 1987). However, orangutans experience relatively low levels of predation risk. The only non-human predators of the orangutan are clouded leopards and Sumatran tigers (van Schaik 1999). Orangutans seem to be able to avoid these predators with relative ease by spending the majority of their time in the trees (van Schaik and van Hooft 1996). Therefore predation risk does not seem to be a major factor determining orangutan sociality. Alternative benefits that have been suggested to account for orangutan associations are largely social, such as mating, the socialisation of infants and protection from harassment from conspecifics (Sugardjito et al. 1987, van Schaik 1999). At Suaq Balimbing, for example, the largest stable parties were found during periods of high mating activity and females with young offspring often formed groups in which infants could socialise (van Schaik 1999). Finally, the presence of forced copulations among orangutans indicates that females and dominant males can benefit from associating, the female to gain protection from harassment by unflanged males and the dominant male to safeguard his reproductive success (Sugardjito et al. 1987, van Schaik 1999).

Given the benefits of grouping, it seems surprising that orangutans spend the majority of their time alone and are the most asocial of the great apes. This asociality has been largely attributed to the harsh ecological conditions present in the South-east Asian rainforest, which is characterised by low productivity (Janzen 1974). Fruit in these rainforests occurs in small, discrete patches; therefore one individual can theoretically deplete an entire patch of fruit on its own (Rodman 1977). Grouping should therefore lead to high levels of feeding competition. Among the African apes, feeding trees are generally larger, and periods of extremely sparse fruit production do not occur to the same levels as in South-east Asia, which can help to explain the more social behaviour

of the African apes (Knott and Kahlenberg 2007). The importance of feeding competition in determining the orangutan social system has been supported by evidence that aggregation sizes are related to the amount of available food (Utami et al. 1997), although this relationship could simply be caused by animals aggregating at a food source and not necessarily socialising. However, travel bands have also been shown to form more often when fruit availability increases (Sugardjito et al. 1987) and average party size is higher at more productive sites (van Schaik 1999). In addition, it has been shown that the age-sex class with the highest energetic costs (females with mid-sized infants who must both carry their heavy infants for long periods and provide them with most of their nutrition) actively avoid company, emphasising the evident costs of association (van Schaik 1999). Finally, in captivity orangutans have been shown to express high frequencies of social behaviour, including regular grooming (Edwards and Snowdon 1980, Poole 1987, Zucker and Thibaut 1995, Tajima and Kurotori 2010). Semi-captive and free-ranging orangutans undergoing rehabilitation also display a range of social behaviours (Salina et al. 2004). Observations at Chester, Cologne and Apenhaul zoos showed that captive orangutans spent an average of 15% of the day in social interactions (Claßen 2011), which far exceeds values found in wild populations, which range between 1-1.5% (Fox et al. 2004, Kanamori et al. 2010). This evidence implies that when the ecological conditions allow it, orangutans do express a relatively high degree of social behaviour. The comparatively solitary nature of the orangutan therefore seems to be an adaptation that maximises foraging efficiency in a relatively unproductive environment (Rodman 1973). However, given more favourable conditions, orangutans do exhibit higher levels of sociality (Edwards and Snowdon 1980).

If the orangutan is indeed living in a relatively harsh environment, this again can help to account for the collapse of the population following the onset of deforestation (Goossens et al. 2006). If fruit productivity is already low, even minor habitat degradation may force this below the limit for orangutan survival.

1.3.3 Activity pattern and diet

Orangutans are the largest primarily arboreal mammal (Knott and Kahlenberg 2007), and have been observed to spend as much as 99% of time in the trees (Wheatley 1982). Males are usually more terrestrial than females (Rodman 1977), but a recent camera trap study suggested that all age-sex classes travel on the ground more than previously thought (Loken et al. 2013). Although this study focussed on only one population, it may suggest that the previous value of 99% arboreality is an overestimate. Orangutans typically leave their night nests at sunrise and spend the day moving between food sources, feeding and resting (Morrogh-Bernard et al. 2009). Orangutans spend very little time engaged in social activities, in particular very little time grooming (Galdikas 1995). The largely solitary lifestyle of the orangutan may preclude the need for grooming, as the social benefits will be less important, and the ectoparasite load of relatively asocial and arboreal individuals is likely to be low (Knott and Kahlenberg 2007). Orangutans build a new nest platform each night (Davies 1986), enter around an hour before sunset and generally remain in it until the morning (Morrogh-Bernard et al. 2009).

Orangutans are primarily frugivorous but they also eat young leaves and shoots, buds, flowers, insects, mineral rich soil and the cambium layer of the bark of many tree and liana species as well as the complete bark of other tree species in times of lower fruit availability (Rodman 1977, Delgado and van Schaik 2000, Morrogh-Bernard et al. 2009). Orangutans have been observed eating meat; one instance of a female eating an

infant gibbon (Sugardjito and Nurhuda 1981) as well as a number of instances of the killing and consumption of slow lorises have been recorded (Utami and van Hooff 1997). However, these observations remain rare and have been attributed to a stumble-upon-and-capture form of predation and not active hunting (Utami and van Hooff 1997). Meat is therefore not considered to be a major component of the orangutan diet.

Orangutan diets are heavily focussed on fruit consumption, which is unusual given their large size (Gaulin 1979). Flanged males weigh an average of 86kg, unflanged males 45kg and females 39kg (Markham and Groves 1990). Assuming an average weight of 55kg, it has been estimated that an orangutan needs to consume an average of 2,333 calories per day (Wheatley 1982). Nutrients and particularly energy are more readily accessible from fruit than other plant parts such as leaves (Cowlshaw and Dunbar 2000); however, orangutans still have to consume large quantities to achieve their energetic requirements. Protein appears to be a strong constraint on the orangutan diet. For example, it was found that the protein to fibre ratio was an important predictor of orangutan preferences for different fruits and flowers (Harrison 2009). Orangutans also preferentially select young leaves that have high crude protein and gain a considerable amount of protein from fruit (Hamilton and Galdikas 1994). Indeed, orangutans have been shown to experience severe shortages in protein when fruit is scarce (Vogel et al. 2011). The reliance of the orangutan on fruit, and the deficiencies they express when they are forced to consume fallback foods, indicates that they do not have the dietary flexibility to adapt to novel conditions. Indeed, this specialised diet is thought to have been one of the main factors that led to the decline of the orangutan from mainland Asia, when fruiting patterns became more unpredictable (Jablonski et al. 2000).

Fruit resources in South-east Asian rainforests are relatively dispersed in both space and time, making these forests lower in overall productivity than other tropical rainforests

(Knott and Kahlenberg 2007). This is exacerbated by the unusual fruiting patterns of the dipterocarp trees that dominate much of the rainforests of Borneo and Sumatra. These trees experience mass flowering and fruiting events that correlate strongly with El Niño events (Curran et al. 1999). During these periods, up to 90% of canopy species can flower and fruit over a period ranging from a few weeks to a few months (Medway 1972). Orangutans gorge themselves on fruit during these periods, often devoting 100% of their feeding time to fruit for a number of days or weeks (Mackinnon 1974, Galdikas 1988, Knott 1998). However, these fruit booms are usually followed by a period of very low fruit availability, as the trees have consumed all of their stored resources in producing fruit (Wright et al. 1999, Holmgren et al. 2001). The orangutans are then forced to consume large quantities of fallback foods, such as leaves and bark, as well as relying heavily on fat that they have stored during the previous fruit boom. Orangutans are believed to be particularly well adapted for fat storage, allowing them to survive the long periods of very low fruit availability (Knott and Kahlenberg 2007). Changes to the frequency of El Niño events that may occur with changing climates could have negative impacts on the orangutan by disrupting this pattern. However, varying levels of fruit availability are not characteristic of all orangutan sites. Peat-swamp forests such as Sabangau, for example, have much smaller fluctuations in fruit availability (Morrogh-Bernard et al. 2009).

1.3.4 Orangutan conservation

Orangutan populations have declined dramatically in the past century in response to deforestation and forest fragmentation, hunting for both bushmeat and the pet trade, and forest fires. The population of Sumatran orangutans is estimated to have dropped by 86% in the last century (Rijksen and Meijaard 1999) to the 6,224 estimated to remain in

the most recent census (Wich et al. 2008). Bornean orangutans are more numerous and Wich et al. (2008) estimate that there are at least 54,000 remaining. This can be divided into around 3,000-4,500 *P. p. pygmaeus*, 35,000 *P. p. wurmbii* and 15,800 *P. p. morio*. The Sumatran orangutan is therefore classified as critically endangered and the Bornean species as endangered by the IUCN (IUCN 2013).

The orangutan has been hunted by humans for hundreds of years, both by the indigenous people of Borneo and Sumatra as well as foreign hunters and collectors who killed and captured orangutans en masse for scientific purposes, as trophies and for zoos (Rijksen and Meijaard 1999). However, legislative protection of the orangutan and its habitat also has a relatively long history. Between 1916 and 1933 the Dutch colonial government in Indonesia became one of the first countries to pass protected area legislation (Jepson and Whittaker 2002) and in 1925 the orangutan became the first officially protected mammal in South-east Asia (Rijksen and Onderzoek 1995). In reality, however, these measures had little impact on the orangutan as hunting continued and intensified (Rijksen and Meijaard 1999).

In 1962 Barbara Harrisson initiated the first orangutan rehabilitation programme (Aveling and Mitchell 1982). In the following decades a number of rehabilitation centres were built and this became a major conservation strategy for the orangutan, aiming not only to rescue and rehabilitate the animals but also to reduce their market value and discourage the trade (Rijksen and Rijksen-Graatsma 1975). These centres quickly became tourist attractions and were criticised for losing their focus on the preservation of the species and for failing to successfully rehabilitate the apes (Lardeux-Gilloux 1995, Yeager 1997). Continued habitat loss increased the number of animals in rehabilitation centres, particularly after the fall of the Suharto regime in Indonesia

which was followed by an intensification of logging and encroachment on orangutan habitat (Nelleman et al. 2007). A new model, termed reintroductions, was therefore developed to deal with these displaced orangutans. The main difference between the new reintroduction model and the old rehabilitation process for orangutans was that in reintroductions, orangutans were only released into areas where there are no wild individuals present, but both terms are now used interchangeably (Rijksen and Meijaard 1999, Russon 2009). Although rehabilitation and reintroduction have been relatively successful in raising awareness about the plight of the orangutan, their major success rests on looking after the animals displaced by hunting and deforestation rather than directly addressing these issues (Russon 2009).

The Indonesian government is now focussing more heavily on law enforcement and protecting orangutan habitat as these issues will clearly be of great importance for the survival of the remaining wild populations (Rijksen and Onderzoek 1995, Nelleman et al. 2007). Major conservation organisations are now also focussing on protecting orangutan habitat and halting the pet trade (Orangutan Foundation 2013, WWF 2013). The current status of the orangutan is critical, so there is a clear need for these measures. However, it is also important to look to the future when planning conservation initiatives, and to try to consider the potential effects that threats such as climate change and disease will have on the orangutan in the future. Modelling approaches provide a key tool for this, but to date few models have been applied to orangutan conservation. In one of the few studies to incorporate modelling, Marshall et al. (2009) used a Population Viability Model to look at the effects of inbreeding, hunting and logging on orangutans. This study found that populations required more than 250 individuals for genetic stability, hunting rates exceeding 1% are unsustainable even in prime habitats, and even moderate rates of logging are predicted to drive most populations of orangutans to

extinction within 100 years. The publication of these sorts of predictions allows conservation programmes to implement a longer-term approach rather than simply reacting to current threats.

1.4 Threats to the survival of the orangutan

1.4.1 Deforestation and land conversion

One of the major anthropogenic threats to the survival of the orangutan is land cover change. Humans have had a dramatic impact on land cover across the globe. Over the last 10,000 years, around half of the ice-free land surface has been converted by humans to agricultural or urban systems (Chapin et al. 2000, Lambin et al. 2003). In the past, agriculture in South-east Asia focussed on shifting cultivation, which had relatively limited effects on the tropical forests (Rijksen and Meijaard 1999, Fox et al. 2000). During the colonial period, however, the international trade in timber, palm oil, tobacco and rubber began (Husson et al. 2009). These industries have grown massively over the past few decades and combined with the recent unprecedented rise in human population have caused widespread changes to the natural environment. Deforestation has been rampant in South-east Asia, both for the valuable timber and to convert land into croplands and commercial plantations (Houghton 1994, Achard et al. 2002, Lepers et al. 2005). Between 1990 and 2005, for example, plantation forests in South-east Asia increased in area by 25% (Koh 2007). Peatlands are particularly suitable for palm oil plantations, and around 45% of Indonesia's peatlands have now been converted for this purpose (Smolker et al. 2009). Indonesia and Malaysia rank as the world's largest palm oil producers (Smolker et al. 2009).

The speed, intensity and pervasive nature of this deforestation have been exacerbated by government policies. From 1903 to 1990, for example, the Indonesian government

resettled millions of people from overpopulated islands such as Java to the less densely populated Sumatra and Kalimantan, intensifying pressures on the natural resources in these regions (Rautner et al. 2005). In 1995, more than one million hectares in Central Kalimantan were designated for rice production to feed the people on overpopulated Java. This project not only caused the destruction of vast areas of forest, but also failed entirely as the soil was largely too acidic to grow rice (Aldhous 2004). In addition to the deforestation condoned by the government, large-scale illegal logging operations are common. This illegal deforestation often includes logging in national parks and officially protected areas (Nelleman et al. 2007, Broich et al. 2011). In Kalimantan, for example, between 1996 and 2002, two thirds of deforestation occurred in proposed and existing protected areas (Fuller et al. 2004). These operations are able to continue as a result of corruption and the weak enforcement of forestry laws by the governments (Schroeder-Wildberg and Carius 2003, Measey 2010).

Forest cover in South-east Asia now declines by around 1% per year (Miettinen et al. 2011a). It has been estimated that Borneo lost an average of 850,000 hectares per year between 1985 and 2005 (Rautner et al. 2005). Deforestation is likely to have devastating effects on biodiversity in South-east Asia. Based on extinction data from Singapore, it has been predicted that deforestation will lead to the loss of 13-42% of regional populations of both terrestrial and freshwater taxa in South-east Asia by 2100 (Brook et al. 2003). The orangutan, which relies on tropical forests for its survival, is therefore extremely vulnerable to deforestation. Indeed, genetic evidence suggests that the recent crash in orangutan population numbers can be attributed largely to anthropogenic environmental changes (Goossens et al. 2006). Orangutans have also recently been observed to turn to crop-raiding in degraded habitats (Campbell-Smith et al. 2011b). This leads to conflict with the farmers, who may resort to killing the orangutans to

protect their farmlands. As habitats become increasingly degraded and more orangutans become reliant on crop-raiding, this issue is likely to become more important.

1.4.2 Forest fragmentation

A further threat associated with deforestation is forest fragmentation. Logging often fragments the landscape, leaving patches of primary or degraded forest separated by agriculture or plantations. This can have severe consequences on the productivity of both the remaining forest fragments and the areas of logged forest; for example, an eight year study of dipterocarp trees in both Gunung Palung National Park and the surrounding areas of logged forest found that the trees in both areas experienced widespread recruitment failure (Curran et al. 1999). Fragmentation can have severe consequences for species survival. Fragmentation often isolates small populations, increasing the risk of extinction (Cowlshaw and Dunbar 2000). Stochastic variation in fecundity and mortality and seasonal fluctuations in environmental conditions can have a far greater impact on smaller populations, which have a higher risk of population collapse (Lande 1988). Small populations are also more vulnerable to the loss of genetic diversity through genetic drift (Cowlshaw and Dunbar 2000) and have potentially reduced survival chances as a result of inbreeding (Ledig 1992). At low population sizes the Allee effect can also become important; when a population declines to a certain size the growth rate becomes negative and the population will consequently become extinct (Chen and Hui 2009). Fragmentation can also affect the microclimate, while edge effects can lead to changing conditions at the edges of forests (Fischer and Lindenmayer 2007). By creating small, separated populations, fragmentation can therefore have a critical influence on species survival.

Many primate species are vulnerable to fragmentation, as fragments may be too small to support the populations needed for long-term survival (Chapman et al. 2006). Even if the patch size is sufficient for the survival of a viable population, fragmentation can act in concert with other anthropogenic effects to cause further population declines. The opening up of forest regions increases the accessibility of the forest for hunting, harvesting of forest produce and the capture of primates for the pet trade (Marsh 2003). In addition, this increase in proximity to humans can potentially increase inter-specific disease transmission (McMichael 2004, Patz et al. 2004). Animals may also be forced to traverse areas inhabited or used by humans and their livestock, in order to move between patches, which again may increase the risk of disease transmission (Gillespie and Chapman 2008). This is particularly relevant for large species with large home ranges such as orangutans, which may struggle to survive in a single fragmented patch. Fragmentation may also introduce or increase the size of rodent populations which may carry emerging diseases (Chen et al. 2011). Habitat fragmentation has indeed been shown to be an important causal factor in disease outbreaks in wildlife in the USA (Dobson and Foufopoulos 2001). Among primates, there is some evidence to suggest that individuals in fragmented landscapes are more likely to be infected with parasites. Red colobus monkeys (*Procolobus rufomitratu*s) inhabiting forest fragments in Uganda, for example, were found to harbour a greater number of gastro-intestinal parasites than those in unfragmented forest – although this was not the case for black-and-white colobus, *Colobus guereza* (Gillespie and Chapman 2008). Of the five species of parasite found among the red colobus monkeys living in both the fragmented and the unfragmented forests, four were found at a higher prevalence among the monkeys in the fragmented forests (Gillespie and Chapman 2008). Humans and livestock in a village close to Kibale National Park harboured *Escherichia coli* bacteria that were

significantly more similar genetically to those from primates living in forest fragments near Kibale than those from primates within the park, and this similarity increased in the more disturbed fragments (Goldberg et al. 2008a). These studies indicate that forest fragmentation, probably through its effect on increasing contact between humans and primates, can increase the prevalence of parasites and bacteria.

1.4.3 Hunting for bushmeat and for the pet trade

The hunting of primates for bushmeat is a common occurrence that represents a major threat to primate biodiversity (Bradshaw et al. 2009, de Thoisy et al. 2009). The recent opening up of logging concessions has exacerbated this threat, as logging improves human access to the forests (Husson et al. 2009). Human population growth has meant an increase in the number of hunters, leading to more intense hunting pressure (Sodhi et al. 2004). Ape bushmeat is eaten by numerous groups of indigenous people, but in recent years an active international trade has also developed (Bowen-Jones 1998, Nijman et al. 2011). In addition to food, primates are widely hunted for medicinal purposes, skin or other body parts for ornamentation, sport, for pets or for entertainment purposes or because they are agricultural pests (Mittermeier 1987). The live capture and transport of primates is particularly damaging to population numbers, as mothers with young infants are the preferred targets. This way a hunter can obtain an adult carcass for meat, skin or other body parts, and an infant to sell on the live market (Mittermeier 1987). Mortality rates of these infants are high, with death resulting from infection, stress or being fed inappropriate food; thus, for every infant that survives to its final destination (e.g. zoos, resorts, entertainment facilities), many more will have died in transit (Shepherd 2010).

Hunting is therefore a severe threat facing primate species worldwide, including the orangutan. Orangutans have been hunted by the indigenous people of Borneo and Sumatra for food in the past (Medway 1977, Harrison 1996, Rijksen and Meijaard 1999), and this continues today (Marshall et al. 2006). Orangutans are also hunted for their body parts; for example, the ban on human head-hunting led to increased hunting of orangutans for their skulls as a substitute for human skulls (Rautner et al. 2005). In addition, orangutans are the most commonly used non-human primate in entertainment at zoos, parks and resorts in South-east Asia, and are commonly used in photography sessions (Agoramoorthy and Hsu 2005). Orangutans are also kept and sold as pets both nationally and internationally (Nijman et al. 2008, Nijman and Asia 2009).

1.4.4 Forest fires

Forest fires represent a serious risk for the rainforests of Borneo and Sumatra. Logging and forest degradation considerably increase the susceptibility of forests to fire (Siebert et al. 2001, Dawson et al. 2002), while land burned in a previous fire is particularly sensitive to future fires (Taylor et al. 1999). Climate change may also increase the risk of fires by causing El Niño events to become increasingly common (Parry et al. 2007). El Niño brings severe droughts which increase both the frequency and extent of fires (Suhud and Saleh 2007).

The effects of fire on tropical ecosystems are diverse. Smoke causes health problems for local wildlife and kills new seedlings (Wuethrich 2000). The dramatic fires of 1997/8 caused the temporary extirpation of more than 100 butterfly species at one site in Borneo and if fires occur more frequently than the time required for population recovery, fires will gradually result in extinctions (Charrette et al. 2006). Siamang family groups living in a region affected by fire had lower infant survival, probably

related to a lower availability of figs in their range (O'Brien et al. 2003). Finally, orangutans may be particularly vulnerable as the trees that they rely on take many years to grow; therefore forests ravaged by fire may take many years to recover to a level suitable for orangutan habitation (Dawson et al. 2002).

1.4.5 Climate change

In the coming century, global temperatures are predicted to increase by as much as 6.4°C, rainfall patterns will change and extreme weather events may become more common (Solomon 2007). These climatic changes are likely to have severe impacts on species survival; for example, it has been predicted that by 2050, with only mid-range climate warming, 15-37% of a sample of over 1000 species will be 'committed to extinction' (Thomas et al. 2004). Climate change is also likely to have a strong impact on the behaviour and distribution of species across the globe. Ranges are likely to shift, causing a major problem for conservation organisations, particularly in areas where species ranges move outside of currently protected areas. Significant range shifts towards the poles and the advancement of spring events have already been observed in a number of species (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2005). Ranges are also likely to move towards higher elevations; for example, in Madagascar, there is evidence that 30 species of reptiles and amphibians have shifted their ranges upslope in response to climate change (Raxworthy et al. 2008). Food quality and availability will change with the climate, leading to behavioural changes in species forced to adapt. The composition of species at sites across the world will change, with some species increasing while others decrease in abundance (Walther et al. 2002). New combinations of species cohabiting in particular environments will also occur, as species' responses to climatic change are likely to vary in both speed and degree (Bush

and Hooghiemstra 2005). Species compositions at certain sites have already been observed to have changed, with species from lower latitudes increasing in abundance while those from higher latitudes decline (Parmesan 2005, Wilson et al. 2007). Thus, climate change has the potential to cause dramatic changes to species distributions, composition and behaviour across the world, which is likely to create challenges for conservation efforts. Predicting these potential changes could assist conservation organisations to prepare for future conditions and thereby help to prevent loss of global species diversity.

Predictions suggest that both chimpanzees and gorillas are likely to be vulnerable to climate change, with large contractions and shifts in their distribution patterns and behaviour predicted (Lehmann et al. 2010a). One of the main explanations proposed for the collapse of the orangutan range during the Pleistocene is climate change (Jablonski 1998), indicating that orangutans may be susceptible to further climatic change in the future. The orangutan is already living in a relatively unproductive environment so any changes that reduce this productivity further could have important ramifications (Suhud and Saleh 2007). Climate change may also lead to a further intensification of human pressures on orangutan habitat as rising sea levels will reduce the area of land available for agriculture (Mimura et al. 2007) and probable increases in the frequency of forest fires will destroy large tracts of rainforest (Ardiansyah and Putri 2011). Only one study has looked at the potential effects of climate change on the orangutans to date; this focussed on populations in Sabah and found that suitable habitat is likely to shift westward, while orangutan abundance may decrease across currently occupied areas by 2100 (Gregory et al. 2012). A broader analysis of the effect of climate change across the entire distribution is clearly required to gain a more detailed insight into the extent of this threat.

1.4.6 Disease

The great apes are particularly threatened by disease because of their susceptibility to human diseases and their slow life histories. Diseases, whether human-related or not, have had devastating effects on a number of African ape populations over the past few decades. Of particular repute, the Ebola virus killed a huge number of the gorillas in West Central Africa; for example, at Lossi National Park in the Republic of Congo it has been estimated that around 5000 gorillas died from Ebola during 2002 and 2003 (Bermejo et al. 2006). Ebola also struck the chimpanzee community living in the Tai forest in the Ivory Coast (Boesch 2008). A polio-like disease and mange both affected the Kasekela community of chimpanzees at Gombe in Tanzania, while respiratory epidemics have been observed at numerous chimpanzee and gorilla sites (Cranfield 2008, Kaur et al. 2008, Kaur and Singh 2008, Koendgen et al. 2008, Pusey et al. 2008). In fact, most illness related deaths in the Kasekela community could be attributed to respiratory diseases (Williams et al. 2008). There is evidence to suggest that some of these diseases may have been transmitted from human sources (Kaur et al. 2008).

Information on disease outbreaks in orangutans is more limited than for the African apes, as habituation for research and tourism is less widespread in this taxon (Woodford et al. 2002). However, this is not to say that disease does not pose a serious risk for the future survival of the orangutan, a risk that will increase as humans and orangutans are forced into closer proximity in the future. Wild orangutans have been observed to harbour a range of intestinal parasites (Mackinnon 1974, Collet et al. 1986, Mul et al. 2007), malaria (Reid et al. 2006) and viruses such as Hepatitis B (Warren et al. 1999), dengue and Japanese encephalitis (Wolfe et al. 2001, Kilbourn et al. 2003) among others. As research into orangutan disease increases, the current list is likely to expand

considerably. Significant differences have been found in pathogen exposure between free-ranging (in Tabin Wildlife Reserve) and semi-captive (undergoing rehabilitation at Sepilok Orangutan Rehabilitation Centre) orangutans, indicating that environmental factors can have important implications for disease (Kilbourn et al. 2003). In addition, (Wolfe et al. 2002) found that malaria was significantly more common among the semi-captive orangutans at Sepilok than in the free-ranging orangutans in the Tabin Wildlife Reserve. It is suggested that this may be the result of the extremely high population density at Sepilok ($\sim 100/\text{km}^2$ compared to $\sim 2/\text{km}^2$ in the wild) leading to increased disease transmission. Increased disease spread at higher densities could have important implications for the future survival of the orangutan; as forest fragmentation increases it is likely that orangutans will be forced to live at higher densities in the remaining habitat patches.

There is also evidence that ecotourism may pose disease risks for the orangutan. At Sepilok rehabilitation centre, for example, it was found that a considerable proportion of the visitors were ill and potentially infectious (Muehlenbein et al. 2010). At Ketambe in Sumatra there is evidence that both an influenza type disease and conjunctivitis passed from the human attendants to the rehabilitant orangutans, and in the case of the influenza, this was then passed on to two wild orangutans (Rijksen 1978).

Climate change may pose a risk in terms of its impact on disease as it is likely to affect disease dynamics across the globe (Harvell et al. 2002). Tropical regions already harbour greater pathogen species diversity than more temperate regions (Guernier et al. 2004). For example, the diversity of protozoa that affect primates increases closer to the equator (Nunn et al. 2005). An expansion or intensification of these warm, wet conditions will have important implications for disease. The prevalence and severity of infectious diseases affecting most primates is likely to increase as temperatures increase

(Chapman et al. 2005). The climate may influence disease both directly and indirectly; by directly impacting on the distribution of pathogens and their vectors and by influencing the nutritional and demographic status of host populations, making them more or less susceptible to disease (Patz et al. 1996). If climate change negatively impacts upon the distribution of fruit in the South-east Asian rainforests and provides a climate more conducive to pathogens, the orangutan will become increasingly vulnerable to disease. Thus, disease risk is clearly a significant conservation concern for the orangutan that is likely to become more important in the future as habitat loss, increased proximity to humans and climatic changes increase the risks of disease transmission. However, the level of this threat to wild populations and the value of possible preventative measures have been largely unexplored.

1.5 The value of modelling

There are clearly a range of areas regarding the future conservation of the orangutan that need to be investigated, and modelling approaches provide a useful technique to do this. Within primatology, modelling approaches have yet to be widely utilised. In a review paper, Dunbar (2002) described a range of different modelling techniques and highlighted the ways in which these methods could be applied to primate studies. In the following years, three particular modelling techniques have gained momentum and have been increasingly utilised by primatologists. These methods are time budget models, first applied by Dunbar (1992a), social network analysis, which has been applied largely to studies of primate social structure (Lehmann and Boesch 2009, Ramos-Fernandez et al. 2009, Brent et al. 2011a, Brent et al. 2011b, Kanngiesser et al. 2011, Lehmann and Ross 2011), and agent based models, which have been used to address questions ranging from disease transmission (Nunn et al. 2008) to foraging strategies (Ramos-

Fernandez et al. 2006). Modelling approaches allow for the investigation of questions that would not be possible in a field based project, such as the use of time budget models to predict the effects of climate change on a species (Dunbar 1998). Modelling provides a means of performing analyses that could be considered to be unethical, impractical or prohibitively expensive under natural conditions. The analysis of disease transmission, for example, has been greatly facilitated by the development of both social network analysis and agent based models. These models allow us to simulate the spread of disease across networks (Guimarães et al. 2007) or whole populations (Nunn et al. 2008), to artificially remove particular individuals from networks (Lusseau 2003) and to model the effect of seasonal changes on predicted disease spread (Cross et al. 2004). Attempting to perform these studies in the field would clearly be an extensive project involving huge expense and in many cases (such as monitoring the spread of introduced diseases through social groups) would be considered to be unethical.

In this thesis three modelling approaches will be employed, time budget modelling, social network analysis and agent based modelling, to address questions regarding the importance of habitat, climate change and disease for the conservation of the orangutan. Current and future distribution patterns will be examined using time budget models. Potential disease transmission in a single population of orangutans will be investigated using social network analysis and an agent based model, and the results compared to those from a community of chimpanzees. A comparison with chimpanzees, a species with a similar but more gregarious social system than the orangutan, will provide insights into the risk of disease in orangutan populations living in a more gregarious manner, such as those in rehabilitation centres. The aim is to provide novel information about the vulnerability of both species that will help to guide future conservation measures for both orangutans and chimpanzees.

1.6 The current and future distribution of the orangutan: a time budget approach

An important focus of orangutan conservation is on protecting suitable habitat (Nelleman et al. 2007, Orangutan Foundation 2013, WWF 2013). This requires an understanding of the factors that affect the ability of the orangutan to survive in different environments and to respond to future habitat changes. The current distribution of the orangutan is thought to have been affected by anthropogenic factors such as deforestation and hunting, the presence of geographical barriers to dispersal such as wide, fast flowing rivers and poor quality soil and forest cover, as well as colder and wetter weather at high altitudes (Rijksen and Meijaard 1999, Husson et al. 2009), but the behavioural factors that restrict orangutan distribution patterns remain unknown. The potential response of the orangutan to habitat change also remains largely unexplored. The level of social flexibility predicted for a species can be used as a proxy for its ability to adapt its social system in response to novel conditions (Lehmann et al. 2010a). This provides an indication of the extent to which a species will be able to cope with the environmental changes predicted in the coming decades. In many cases, such as the potentially widespread habitat changes that will be associated with climate change and human population growth, habitat alterations will exceed the limits of social flexibility and species may have to shift their ranges in order to survive. It is imperative that conservation initiatives are able to take this into account and concentrate efforts on areas in which long-term survival will be possible. The expected response of the orangutan to future climate change has been largely unexplored to date, with the only analysis undertaken focussing specifically on Sabah in Malaysia (Gregory et al. 2012). Addressing these gaps in the current literature is clearly necessary to help to improve the scientific basis and effective targeting of conservation action for this species. This

can be achieved using time budget models, a method of exploring the determinants of a species range.

1.6.1 An introduction to time budget models

Time budget models can provide important insights for conservation by helping to elucidate the complex relationship between a species and its environment (Dunbar et al. 2009). These models are based on the view that time is a constraint (Dunbar et al. 2009). Within primatology, this perspective dates back to Altmann (1980) who developed an influential model of maternal time budgets in yellow baboons (*Papio cynocephalus*), noting that females are forced to devote more time to feeding as their infant grows in order to meet nutritional demands. Dunbar & Dunbar (1988) extended this model to show that females are only able to meet these additional feeding time demands by reducing the amount of time that they spend resting, and in extreme situations by cutting back on social time. These early papers were important as they highlighted the inelastic nature of time and the need for animals to balance their time budgets in order to survive. Time was therefore recognised to be a key constraint facing primates. Dunbar (1992a) used this platform to create a model that could predict time budget allocations for the gelada (*Theropithecus gelada*) and from this identify the range of environmental conditions in which it can survive, based on the assumption that a species cannot survive in locations where total time budget allocations exceed the time available in a day.

Time budget models predict the amount of time that a species ought to spend in each of its four key behaviours: feeding, moving, resting and socialising. It is estimated that these activities consume around 95% of the active day (Dunbar 1996). The remaining 5% is spent in activities such as territorial defence, drinking and monitoring the

environment; however, individually these behaviours take up very little time and are therefore ignored for modelling purposes (Dunbar 1996). The amount of time required for each of the four different behaviours is determined primarily by the climate, the environment and demography.

1.6.2 The effect of the climate and the environment on time budget allocations

Feeding time can be affected by the local climate and environment in two different ways; through effects on thermoregulation and on food quality (Dunbar et al. 2009). Increased thermoregulation costs, a result of extreme temperatures or a reduction in the quality of food, can force animals to spend more time feeding in order to meet their nutritional requirements. Japanese macaques (*Macaca fuscata*), for example, living on a cold temperate island spent more time feeding compared to those living on a warm temperate island; it is likely that this was due to an increased amount of energy required for thermoregulation and to lower quality forage caused by the lower temperatures (Agetsuma and Nakagawa 1998). In Africa, higher temperatures can reduce the quality of food; for example, increased temperature leads to increases in gelada feeding time by reducing the quality of grasses (Dunbar et al. 2002). Environmental variables such as altitude and forest cover can also impact feeding time; for example, gelada spent more time feeding at higher altitudes, a result of a combination of increasing temperature-dependent energy requirements and the declining forage quality (Iwamoto and Dunbar 1983). The majority of primates rely on trees for food; therefore the level of forest cover is also likely to affect feeding time.

The climate and the level of forest cover also have a strong impact on the availability and distribution of food, which has evident implications for the time required for moving in order to find sufficient food to meet nutritional requirements (Dunbar 1988).

Resting time has a more complicated relationship with the climate as it is composed of two distinct forms; enforced and uncommitted resting time. Uncommitted resting time is the amount of free time that is not required for other essential behaviours and is therefore likely to be high in prime habitats where animals are not particularly stressed in terms of meeting their time budget allocations. In contrast, enforced resting time is time that animals are forced to devote to resting, for example as a result of thermoregulation or digestion (Korstjens et al. 2010). Under high temperatures and particularly when there is little forest cover, animals may be forced to seek shelter and rest in order to prevent thermal overload, while in cold conditions animals may be forced to rest to conserve valuable energy and minimise the costs of regulating their body temperature (Dunbar et al. 2009). Examples include black-crested gibbons (*Nomascus concolor jingdongensis*), which increased their resting time and decreased travelling time in cold temperatures (Fan et al. 2008), four African ruminant species, which increased resting and decreased feeding and moving times on hot days (du Toit and Yetman 2005) and chacma baboons (*P. ursinus*), which were found to spend more time in sedentary activities such as resting and grooming and less time in feeding as temperatures increased (Hill et al. 2004). Digestion can also force animals to rest, as the activity of digestive enzymes is sensitive to temperature and fermentation can produce heat (van Soest 1982, Dunbar et al. 2009). This is particularly important for folivorous primates as the extraction of nutrients from leaves can require long digestion times during which the animals are forced to remain inactive (Dunbar 1988). The climate and the environment, including variables such as altitude and forest cover, are therefore important determinants of time budget allocations.

1.6.3 The effect of demography on time budget allocations

Climatic and environmental variables clearly affect the time required for feeding, moving and resting; however, in highly social species such as most primates, group living must also be taken into account. Living in groups is thought to be largely an adaptation to reduce predation risk (Dunbar 1988). However, sociality also comes with costs, such as an increase in competition for resources with group mates. In larger groups, resources will be depleted more rapidly, potentially forcing animals to eat a higher proportion of lower quality foods and thus having to spend more time feeding or resting (as lower quality foods require additional digestion times). Brown capuchin monkeys (*Cebus apella*), for example, spent more time feeding in larger groups (Janson 1988), while group size has been shown to be an important positive predictor of feeding time in red colobus monkeys, black-and-white colobus monkeys (Korstjens and Dunbar 2007) and chimpanzees (Lehmann et al. 2007a). Group size has also been shown to be a negative predictor of resting time in vervet monkeys (*Cercopithecus aethiops*; Willems and Hill 2009). Alternatively, animals may need to spend more time searching for additional food patches, thus increasing moving time which in turn requires more energy (Chapman et al. 1995, Chapman and Chapman 2000). Among primates and carnivores, for example, day range was found to be consistently positively associated with group size, indicating that animals in larger groups had to travel further each day (Wrangham et al. 1993). In addition, group size has been shown to be a positive predictor of time spent moving in spider monkeys (*Ateles spp.*; Korstjens et al. 2006), chimpanzees (Lehmann et al. 2007a) and gorillas (Lehmann et al. 2008a).

Group size also impacts strongly on the final time budget component, social time. The frequency of grooming in primates has been shown to correlate positively with group

size and not body size (Dunbar 1991). Time spent grooming has also been shown to correlate positively with group size both within and between primate taxa (Lehmann et al. 2007b). This suggests that grooming also has a social function rather than an entirely hygienic function (Dunbar 1991). It has been suggested that this social function is the maintenance of relationships, contributing to overall group cohesion and integration (Kudo and Dunbar 2001). In larger groups, each individual will have a greater number of relationships to service, which explains why grooming increases with group size. However, time is limited and so grooming time can not increase indefinitely. This hypothesis therefore assumes that at a certain group size, animals will be unable to find the time to service all of their relationships and this may ultimately lead to group fission (Dunbar 1993). This is supported by the evidence that in baboons the probability of group fission increases as the size of the group increases (Henzi et al. 1997). Group size therefore appears to be an important determinant of social time in primates, as grooming is required to maintain relationships and thus prevent the fission of the social group.

1.6.4 Predicting distribution patterns and the factors that restrict distributions

As described above, time budget allocations are considered to be determined by the environment, the climate and demography. This means that mathematical equations can be formulated to predict time budget allocations from climate, environment and group size data. These equations can then be used to predict the distribution of a species. In order to do this, the minimum group size at which the species can survive first needs to be estimated. It has been suggested that for social species there is a minimum group size (set by predation risk) below which the population would not be able to survive, as the costs in terms of predation would be restrictively high (Dunbar 1996). This minimum group size can be estimated from environmental and life history variables (Dunbar

1996, Bettridge et al. 2010) or estimated based on the observed minimum for the species (Korstjens and Dunbar 2007, Lehmann et al. 2008b). Once the minimum group size has been determined, it is possible to predict the distribution of a species using a time budget model. Time budget allocations can be calculated from location specific climate and environmental data, using the minimum permissible group size as the group size value. If the sum of the four time budget components exceeds 100% of the time available in the day, then the group clearly cannot survive in the given environment. If, however, time budget allocations are less than 100% then the species can survive in a group size at least as large as the minimum permissible value. In this way a species distribution map can be created, indicating for all locations whether or not the species is predicted to survive.

Dunbar (1992a) was the first person to apply time budget models to primate distributions, by creating a model of gelada socioecology that could be used to examine the range of environmental conditions under which this species could survive. The model was remarkably successful at predicting the current distribution of gelada. Furthermore, the model showed that outside of the gelada's present altitudinal range, the species would not be able to find enough time for foraging to survive in viable groups. This indicates that their biogeography is limited by foraging time, probably due to the lower quality of forage at lower and higher altitudes. Later models have mapped and investigated the limitations on distribution patterns in baboons (Dunbar 1996, Bettridge et al. 2010), spider monkeys (Korstjens et al. 2006), chimpanzees and gorillas (Lehmann et al. 2008a), red and black-and-white colobus monkeys (Korstjens and Dunbar 2007) and vervet monkeys (Willems and Hill 2009). These analyses provide important insights into the relationship between a species and its habitat and the factors that constrain distribution patterns. Improving current understanding of the reasons why

certain species are unable to live in particular regions and environments is of clear value for their conservation, as it will help to focus resources on the issues that are of prime importance for the continued survival of the species in the areas where they do occur.

1.6.5 Predicting group sizes and social flexibility

Time budget models can also be used to investigate the level of social flexibility available to a species, by exploring the range of group sizes that can be adopted across the distribution of a species (Dunbar 1996). Group size can be increased iteratively in the model and the time budget allocations calculated at each step, until the sum of all four behaviours exceeds 100%. The group size below this final iteration is set as the maximum ecologically tolerable group size (i.e. the maximum possible group size that can be supported in the given habitat). Investigating maximum ecologically tolerable group sizes in this way has provided useful information about the costs and benefits of different grouping patterns in spider monkeys (Korstjens et al. 2006), chimpanzees (Lehmann et al. 2007a) and red and black-and-white colobus monkeys (Korstjens and Dunbar 2007). Looking at the range of group sizes available to a species can also indicate the level of time budgeting stress faced by populations living in different areas, as this reflects the amount of uncommitted time remaining once all essential behaviours have been completed (Korstjens et al. 2010). In areas where animals have a large range of group sizes available to them, animals can respond to habitat deterioration by reducing their group sizes, thereby creating more uncommitted time that can then be allocated to the four essential behaviours. In contrast, in areas where the maximum possible group size approaches the minimum, animals will not have this flexibility and will be highly vulnerable to future change (Lehmann et al. 2010a). The time budget model can be used to predict the range of group sizes available to a species across its

range and also identify areas where this range is predicted to be particularly small and therefore where a species is particularly vulnerable. This information would be useful for orangutan conservation programmes as it will help to focus resources on the areas where the position of the orangutan is the most critical.

The group size actually assumed within the range of realisable values (between minimum permissible group size and maximum ecologically tolerable group size) can also provide interesting information about the relative importance of survival and fecundity in driving the evolution of the social system. A group size approaching the maximum ecologically tolerable value provides benefits in terms of reduced predation, but costs in terms of fecundity due to increased resource competition (Bettridge et al. 2010). Alternatively, groups approaching the minimum permissible group size face greater predation risk and therefore sacrifice survival for increased fecundity (Dunbar 1996). Among baboons, it was found that almost all groups were near the lower limit on group size, indicating that they maximise fecundity over survival (Bettridge et al. 2010). Time budget models can therefore also be used to improve our understanding of the trade-off between these two factors in the evolution of primate grouping patterns.

1.6.6 Predicting the effect of climate change and human population growth

Understanding the factors that influence the current distribution of orangutans is clearly important, but if climate change is as severe as current models predict, the distribution of the orangutan may change dramatically in the future. It is consequently important to explore the potential effects of climate change on both distribution patterns and behaviour and this can also be achieved using time budget models. Climate data predicted for the future can be entered into the time budget models to produce a species distribution map under future conditions. This provides species specific predictions of

the areas which will no longer be suitable for habitation in the future and also those areas that may become newly suitable or remain suitable under climate change (Dunbar 1998). The effects on the individual time budget components can also be quantified to gain an idea of the way in which behaviour is likely to change. These models have been successfully implemented for gelada (Dunbar 1998), chimpanzees and gorillas (Lehmann et al. 2010a), and a general model of African and New World primates (Korstjens et al. 2010) to date. Time budget models also have the potential for the incorporation of human population growth, although this has not yet been attempted to date.

Time budget models therefore provide a useful method of addressing a number of conservation questions which would be impossible to explore using field based techniques. These models have been applied to a number of primate species to date and one ungulate species (Jian-bin 2006), but the orangutan has yet to be studied using this approach. Given the critical situation facing the orangutan it is extremely important to improve current understanding of orangutan distribution patterns, to highlight the areas within their range where they are the most vulnerable and to predict the ways in which climate change and human population growth will impact upon both the distribution and behaviour of the species.

1.7 Disease as a threat to orangutan survival: a social network analysis approach

1.7.1 Potential disease transmission

Diseases can have devastating effects on animal populations and have been a major factor in the decline of both chimpanzees and gorillas in recent years (Bermejo et al. 2006, Boesch 2008). Infectious diseases represent a considerable threat to global biodiversity; however, it is a subject that has been relatively neglected in conservation

biology (McCallum and Dobson 1995, Daszak 2000, Smith et al. 2006). In this thesis, the threat of disease transmission will be investigated in and compared between the orangutan and the chimpanzee.

Current literature on disease transmission in orangutans is extremely sparse. Based on a review of the literature, the only instance in which disease spread to a wild animal has been recorded was the observation of the spread of an influenza-like disease from human attendants, to rehabilitant orangutans, and from them to two wild orangutans that visited the rehabilitation site at Ketambe (Rijksen 1978). The level of threat that disease poses to the orangutan needs to be more rigorously explored. Comparing disease dynamics between the orangutan and a closely related species, the chimpanzee, is an invaluable method of assessing the relative vulnerability of the orangutan to disease and the way in which differences in social structure impact upon this vulnerability. Chimpanzees can also be seen as a good model for more gregarious orangutans, such as those in captivity or rehabilitation centres. The chimpanzee results may therefore provide an indication of the risk of disease to these populations.

In order to make this comparison there are a number of questions that need to be explored in both species. Firstly, it is important to predict the ability of disease to spread between individuals and the likelihood of it reaching epidemic proportions. The role of particular individuals in disease spread also needs to be investigated. Certain individuals may play a more important role in disease transmission (Lloyd-Smith et al. 2005), in which case it is essential that these animals are identified. If an outbreak occurs, these individuals could be vaccinated and subsequent disease transmission considerably reduced as a result (Newman 2003b). Finally, the transmission dynamics of different types of diseases need to be explored, to highlight the sorts of diseases that pose the most serious threat. Addressing these questions using a field approach would be

difficult, as well as potentially expensive and unethical. Modelling approaches, in this case social network analysis and agent based modelling, do not suffer from any of these problems and so provide an alternative methodology through which to investigate potential disease transmission.

1.7.2 Chimpanzees as a comparison species

Chimpanzees are a good comparison species for the orangutan as they are closely related, yet differ in a number of key respects that are likely to affect disease spread. It has been estimated that the two species diverged around 12 to 15 million years ago (Goodman et al. 1998, Glazko and Nei 2003) and so they retain many similarities, such as large body size, a primarily frugivorous diet and a slow life history (Delgado and van Schaik 2000, Mitani et al. 2002). They also have similar social systems; both species exhibit a form of individual-based fission-fusion social organisation in that they are often found in small parties that vary regularly in composition (Pepper et al. 1999, van Schaik 1999). Similar to the orangutan, the grouping patterns of the chimpanzee seem to be a response to ecological constraints. Chimpanzees primarily eat fruit, which is dispersed in small, discrete patches. This means that chimpanzees in larger groups have to travel greater distances than those in smaller groups in order to find sufficient fruit patches to meet the nutritional requirements of the group (Chapman and Chapman 2000, Wrangham 2000, Williams et al. 2002). It is therefore advantageous for chimpanzees to split into smaller groups to reduce travel costs. Additional travel costs are particularly problematic for females, which tend to travel considerably slower than males; this helps to explain why females are often less gregarious than males (Wrangham 2000). Living in a fission-fusion social system thus allows chimpanzees to obtain some of the benefits of living in a large community (such as increased mating opportunities or improved

territorial defence) without incurring the costs in terms of travel time (Chapman et al. 1995, Lehmann et al. 2007a). Thus, both species are characterised by a form of fission-fusion social organisation, apparently in response to ecological constraints.

However, there are a number of key differences between the two forms of fission-fusion that are likely to have important impacts on disease dynamics. Chimpanzees, for example, appear to live in a more fixed community than orangutans. Communities are clearly defined and interactions between neighbouring communities can be extremely hostile (Watts and Mitani 2001). At Gombe, for example, one group systematically killed all of the males in the neighbouring group, leading to its extinction (Pusey et al. 2007). All members of a community are rarely found together; instead individuals form smaller parties, usually averaging between five and eight independent individuals, depending on the site and the size of the community (Chapman et al. 1994, Boesch 1996, Newton-Fisher 1999). This is much larger than the average party size in orangutans, which tends to be either one or two individuals (Sugardjito et al. 1987, Bastian et al. 2010). Chimpanzee party composition changes regularly, for example every 19 minutes at Budongo (Reynolds 2005) and every 17 minutes at Taï, with mixed sex parties being the most common (Boesch 1996). Chimpanzee males are the philopatric sex while females generally disperse at maturity (Mitani et al. 2002). Relationships between males, many of whom are likely to be related, tend to be much stronger than those between females and most grooming interactions are observed between males (Sugiyama 1969, Pepper et al. 1999). Chimpanzees spend a relatively large proportion of their time in association with others; for example at Taï, individuals spend only 17.6% of their time alone (Lehmann and Boesch 2004). This compares with around 80% for orangutans (Galdikas 1985a). It is therefore apparent that there are similarities between the social systems of the two ape species, but that chimpanzees are

considerably more gregarious than orangutans. It will be interesting to see how this translates into differences in fine-grained social structure and consequently in predicted disease dynamics. Comparing the results for the orangutan with those from the chimpanzee also provides the opportunity to assess the relative vulnerability of the two species to disease.

Furthermore, as orangutans may in the future be forced to live at higher densities, either in small fragments of forest or in rehabilitation centres, analysing disease spread in the more social chimpanzee may provide an indication of the vulnerability of these potentially more gregarious populations of orangutans to disease. At Sepilok Orangutan Rehabilitation Centre (SORC) for example, young orangutans are kept together in nursery groups (Russon 2009), while healthy individuals over three years old are released into a 42km² forest reserve following a quarantine period. There are two feeding platforms within the forest where provisioning takes place twice a day, at the same time each day (Kuze et al. 2008). A similar system was run at Camp Leakey in Tanjung Puting (Russon and Galdikas 1993), and provisioning also continues for orangutans released into Sungai Wain Protection Forest (Russon 1998) and Kaja Island in Central Kalimantan (Russon et al. 2007). This system leads to a more gregarious form of fission-fusion than observed in wild orangutans, as many individuals congregate at the feeding platforms on a regular basis; in 2004, an average of nine orangutans visited each platform at each feeding time in SORC (Kuze et al. 2008). In addition, at Kaja Island individuals were often found to congregate and nest overnight at feeding platforms (Russon et al. 2007). Thus, reintroduced orangutans and those at rehabilitation centres appear to be more gregarious than those in the wild. Analyses of chimpanzees should provide valuable insights into the impact of increased gregariousness on

potential disease transmission and thus on the threat that disease poses to rehabilitant and reintroduced orangutans.

Chimpanzees are also a good comparison species with respect to conservation, as they are currently subjected to similar pressures as the orangutan. There are four recognised subspecies of the common chimpanzee; the western chimpanzee (*P. troglodytes verus*), the Nigerian chimpanzee (*P.t. vellerosus*), the central chimpanzee (*P.t. troglodytes*) and the eastern chimpanzee (*P.t. schweinfurthii*), distributed across 21 countries in Equatorial Africa (Nellemann and Newton 2002, Grubb et al. 2003). The chimpanzee is classified as endangered (IUCN 2013) and there are currently estimated to be between 21,000-56,000 western chimpanzees, 5,000-8,000 Nigerian chimpanzees, 70,000-117,000 central chimpanzees and 76,000-120,000 eastern chimpanzees remaining (Butynski 2003). Chimpanzees are threatened with hunting for bushmeat and the pet trade, habitat loss and fragmentation, and disease transmission (Plumptre and et al. 2010). It has been estimated that thousands of chimpanzees are killed every year for bushmeat (Weiss and Wrangham 1999). Since the 1980s, sanctuaries for chimpanzees have increased considerably in number, and around a third of the chimpanzees in these sanctuaries were rescued or confiscated from the pet trade (Farmer 2002). Habitat destruction and fragmentation are also major concerns and by 2032 it has been predicted that less than 10% of African ape habitat will remain free of the impacts of human development (Nellemann and Newton 2002). Finally, disease transmission has had devastating consequences on chimpanzee populations over the last few decades. Ebola has caused widespread fatalities in western Africa (Huijbregts et al. 2003), while respiratory diseases have spread throughout habituated groups, potentially from human sources (Cranfield 2008, Kaur and Singh 2008, Koendgen et al. 2008, Pusey et al. 2008, Williams et al. 2008). Hence, chimpanzees are also seriously threatened with extinction

and so any information gained about the impact of potential disease transmission in this species will be of great value for their conservation.

1.7.3 Using social network analysis to investigate disease risk

Exploring disease risk in both orangutans and chimpanzees can be achieved using social network analysis, a framework that is used to describe social structure (Brent et al. 2011a). The visualisation of a social network dates back to the early 1930s when Moreno created the first sociogram to depict human relationships (Moreno 1934, Wasserman and Faust 1994). The evolution of social network theory proceeded slowly over the next few years, but recent advances in computing power have initiated a dramatic increase in the use of these modelling approaches in a wide variety of disciplines (Jacobs and Petit 2011). A social network is a graphical depiction of an interaction matrix that is comprised of nodes (represented by symbols) and edges (lines connecting the nodes). Nodes commonly represent individuals in a population and edges the interactions between them, for example grooming or simply association (measured by proximity or presence in the same group). These interactions can be viewed as possible pathways for disease transmission. Visualising the network can provide useful information regarding the relationships/disease pathways within the group, but social network theory can also be used to analyse particular properties of a network and gain a deeper understanding of the underlying social structure and how this may affect the overall spread of disease (Croft et al. 2008). Social network analysis has to date been used to investigate the properties of a wide variety of networks, ranging from online social networks comprising millions of nodes (Mislove et al. 2007) to the far smaller networks found in animal societies (Croft et al. 2008).

1.7.4 Assessing vulnerability to disease and identifying superspreaders

Assessing the overall vulnerability of a population or community to disease and the role that different individuals will play in future disease spread is important for both the most efficient allocation of conservation resources and the selection of the most effective prevention measures. This can be achieved using a range of specific methodologies based on the social network framework. Network measures, for example, can provide useful indications of the vulnerability of social groups to disease. Properties of the overall network structure may be important for disease transmission; for example, disease is likely to spread much faster in networks with lots of connections between individuals than in networks with very few connections (Croft et al. 2008). Identifying how susceptible both the orangutan and the chimpanzee are to disease will help to prioritise disease in the list of threats facing the species. In addition to overall network properties, individual measures can provide useful information about disease dynamics. Individuals with a lot of contacts relative to other group members can be identified; these are likely to play an important role in transmitting disease to a large proportion of the network (Krause et al. 2007, Croft et al. 2008). These individuals have been labelled ‘superspreaders’ (Lloyd-Smith et al. 2005). The identification of superspreaders could be very important for vaccination programmes, as targeting a few highly influential individuals could potentially considerably reduce disease spread and clearly will not require the resources, or be as invasive, as measures aimed at an entire population (Haydon et al. 2006).

The potential benefits of targeting superspreaders for vaccination can be quantified by simulating the removal of superspreaders from the population and comparing the impact on network structure to that calculated when random individuals are removed (Lusseau

2003). If the network fragments more following targeted removals than random removals, this indicates that the targeted vaccination of superspreaders could have a greater impact on reducing disease spread, as a more fragmented network will be associated with fewer potential disease pathways (Newman 2003b). Removal simulations have already shown that a range of species are more susceptible to targeted than random removals (Lusseau 2003, Lusseau and Newman 2004, Manno 2008, Chaverri 2010, Kanngiesser et al. 2011); however, this type of analysis has not been performed on orangutans or wild chimpanzees. Removal simulations also provide an assessment of the vulnerability of a group to member loss. If the network fragments considerably under either form of removal, this indicates that losing individuals (for example as a result of death from disease) could have negative effects on the group by disrupting the structure of their society (Manno 2008).

1.7.5 Simulating the spread of different types of disease across a social network

Diseases with different levels of infectiousness or varying times to recovery are likely to lead to epidemics with differing properties. Predicting the consequences of outbreaks of different types of diseases will provide conservationists with advanced warning of the likely outcome of an epidemic. Although the spread of a number of different diseases has been observed in both chimpanzees and orangutans (Rijksen 1978, Kilbourn et al. 2003, Boesch 2008, Kaur and Singh 2008, Koendgen et al. 2008, Pusey et al. 2008) collecting detailed observational data on the actual patterns of spread for a wide range of diseases would be extremely time and resource intensive and so has not been possible to date. This can be estimated, however, by simulating the spread of disease across a social network using a susceptible-infected-recovered (SIR) model. These models separate a population into three categories of individuals, susceptible, infected and

recovered (Kermack and McKendrick 1927). The model involves discrete time steps, so at each time step the status of individuals is recalculated. At first, all individuals are in the susceptible class. Disease is introduced to a random individual in the network, who transfers to the infected class. At each subsequent time step, disease spreads from infected individuals to their contacts with a probability equal to the product of the infectiousness of the disease and the proportion of time that the two individuals have been associating. Individuals recover at each time step according to the probability of recovery. As a result, the spread of disease is determined by both the parameters of the disease and the social interactions present in the network.

SIR models can be used to investigate a number of interesting features of disease spread in association networks (Cross et al. 2004, Guimarães et al. 2007). Firstly, the spread of disease across the association network can be compared against that on both a network in which individuals' associations are randomised and a network in which all individuals have an equal probability of associating (Cross et al. 2004, Guimarães et al. 2007). This provides an indication of both the susceptibility of the population to disease as well as the importance of including the correct structure of the network for producing accurate predictions (Moreno et al. 2002). The spread of diseases with varying parameters can be simulated and the role of superspreaders in disease spread as well as the value of vaccinations explored in greater depth using SIR models. If certain individuals are both more likely to infect others and more likely to become infected in the simulations, they can be viewed as superspreaders. Vaccinations can be simulated and the change in the predicted overall size of the epidemic calculated. In this way, SIR models can provide invaluable information as to the susceptibility of different social groups and species to different types of disease, and the way in which the structure of their society impacts upon the risk of becoming infected.

1.7.6 Dynamic models: social networks and agent based models

Network epidemiological models can be either static or dynamic; static models simulate disease spread on one network based on data collected over the entire sampling period, while dynamic models use a sequence of networks, each based on a shorter period of time (Cross et al. 2004). Dynamic models thereby incorporate short-term changes in association patterns. Results from dynamic models can be compared to static ones to determine the influence of short-term variation in association patterns on predicted disease spread. These dynamic models, however, require considerable amounts of data, which were not available for the orangutan. Where there is not sufficient data to build a dynamic model, it may be useful to create an agent based model. Agent based models are composed of agents, which represent the individuals, and patches, which represent patches of the environment, for example clumps of feeding trees (Railsback and Grimm 2011). Individuals follow simple rules that are programmed into the model based on what is known about the behaviour of the species in question; for example, they could be programmed to always move towards the patch with the most fruit. Individuals can then be infected with disease, which then spreads between individuals when they come into contact, for example when they are both present on the same patch. In this way the spread of disease between individuals can be simulated at a much finer temporal resolution but without the requirement of in-depth association data. Investigating the spread of disease at this higher temporal resolution, using a dynamic network model for the chimpanzee and an agent based model for the orangutan, will highlight the influence that short-term changes to association patterns have on model predictions.

Thus, social network analysis and agent based models can provide valuable information about disease spread between individuals. These methods have not yet been applied to

orangutans and the results should provide novel and valuable information regarding disease transmission in both species of great ape. This should provide species specific information that could be of value in informing future conservation efforts while also improving current understanding of the way in which differences in social structure impact relative disease risk (Altizer et al. 2003).

1.8 Aims and research questions

The survival of the orangutan is very uncertain and will to some degree depend on the ability of conservation organisations and governments to develop and implement effective conservation plans. Improving the available information from which to create these plans is critical to success. In this thesis, three major modelling approaches are used to address a range of questions regarding the conservation of the orangutan.

Regarding both current and future distribution patterns of the orangutan and employing the time budget modelling approach, five questions are addressed:

1. Which factors currently limit orangutan distribution patterns? (Chapter 2)
2. Do orangutans have limited social flexibility, in terms of the range of group sizes that they can adopt across their range? (Chapter 2)
3. Are there areas where orangutan social flexibility is particularly limited, and therefore where the orangutan may be particularly vulnerable? (Chapter 2)
4. How will climate change affect orangutan distribution patterns and behaviour? (Chapter 3)
5. How will human population growth affect orangutan distribution patterns? (Chapter 3)

Regarding disease transmission and employing social network analysis and agent based modelling, six questions are addressed:

1. Are orangutans and chimpanzees susceptible to the spread of disease? (Chapter 4)
2. Are potential superspreaders (individuals with a disproportionately central position in the network) present? (Chapters 4 and 5)
3. Is vaccination a useful method of limiting disease spread? (Chapters 4 and 5)
4. Does the topology of the social network affect predicted disease spread? (Chapter 5)
5. Do orangutans and chimpanzees have varying susceptibility to different types of diseases? (Chapter 5)
6. Do short-term changes in social relationships affect disease spread? (Chapter 5)

2. Ecological Constraints on the Biogeography and Sociality of the Orangutan

2.1 Introduction

2.1.1 Orangutan distribution patterns

The distribution of the orangutan has experienced a dramatic reduction since the Early Pleistocene, driven by a combination of climate change and the impact of the arrival and expansion of human populations (Jablonski 1998, Delgado and van Schaik 2000, Goossens et al. 2006). Despite the dedication of conservation organisations and government departments to reducing deforestation and bringing a halt to the pet trade, these factors continue to destroy remaining populations (Nelleman et al. 2007). As habitats become increasingly fragmented and degraded, it is essential to gain a detailed understanding of the specific habitat needs of the orangutan, so that conservation resources can be focussed on the most appropriate areas and issues.

A comprehensive understanding of the habitat needs of a species requires some knowledge of the factors that restrict its distribution; it is important to know why a species lives in a given environment, but also why it does not live in others. In addition

to geographical barriers, the ultimate determinants of distribution patterns are the climate and the environment. However, to gain a more detailed understanding of the distribution of the species, it is useful to look at the proximate restrictions on survival, such as behaviour, which interfaces between the climate/environment and the ability of a species to survive (Lehmann et al. 2008a). For example, if feeding trees are widely spaced in the environment, in order to find enough food to meet its energetic requirements an animal may have to spend more time moving than is available. Understanding the behavioural limitations on survival can provide a more in-depth view of exactly how the environment restricts orangutan survival.

It is not only distribution patterns that can be restricted by behavioural time constraints; in primates, group size can also be affected. Orangutans are relatively solitary animals, and it is thought that this is because the ecological costs of grouping are restrictively high (Sugardjito et al. 1987). These costs could include feeding competition or additional travel time in order to find enough food for every individual in the group. If this is the case, orangutans may be living in a relatively unproductive environment and so may be particularly vulnerable to habitat degradation. It is therefore important to investigate this in more depth, to elucidate if it is indeed ecological costs that act to limit orangutan grouping patterns, and if so, what mechanism underlies this.

Finally, orangutan habitat continues to be diminished at a rapid pace. It will not be possible to protect all remaining habitat and so choices will have to be made as to where efforts and resources should be focussed. This will evidently be influenced by proximity to towns and roads, vulnerability to logging and the value of the land for more commercial purposes. However, it would be useful also to have an indication of the ecological suitability of the land for the orangutan, so that areas where the orangutan

has the greatest chance of survival are preserved in preference to those where the position of the orangutan is more precarious.

These issues regarding orangutan habitat suitability need to be addressed, to help to focus conservation resources for this species. Time budget modelling provides a powerful means to do this. Time budget models can be used to investigate how the environment, through its effects on behaviour, shapes biogeographical distributions and social organisation (Dunbar 1992b). These models provide valuable insights into the factors that determine the habitats in which a species can live, the group sizes that they can adopt, and the amount of time budgeting stress that they face in any given environment (Dunbar et al. 2009). Time budget models can therefore be used to provide important information for conservation planning.

2.1.2 Time budget models

Time budget models are based on the assumption that time is an important constraint that can affect a species' ability to survive in a given habitat. For an animal to survive in a given location it must be able to perform all of its essential activities within the time available (Dunbar 1992b).

Time budget models utilise existing relationships between climatic, dietary and demographic variables, and their effects on behaviour, to predict the amount of time that animals would need to devote to each activity under different environmental and climatic conditions (Dunbar et al. 2009). In addition, because most primates are social, the size of the social group needs to be factored into the models. Group living provides benefits such as a reduction in predation risk; therefore, maintaining a social group larger than the habitat specific minimum (set by the level of predation risk) may be an essential part of a species' survival strategy (Bettridge et al. 2010). Grouping, however,

leads to an added demand on time, namely that required for social interaction to maintain group cohesion (Lehmann et al. 2007b). Group size can also affect other time budget components, for example through competition for food, leading to an increase in feeding, moving or resting time (Dunbar 1996). Time budget models take these effects into account and can thereby be used to calculate the group sizes at which a species could persist in a given location (Dunbar et al. 2009). The group size at which all available time has been allocated to time budget demands is the maximum ecologically tolerable group size that can be adopted in a specific location (Dunbar 1992a). If this maximum exceeds the habitat specific minimum, then the species is predicted to survive in the given location.

2.1.3 Biogeography

Time budget models can be used to produce a distribution map for a species, indicating all locations across a specified region in which the species is predicted to live. This map can then be used to examine the factors that restrict the range of the species in question. If a time budget variable is considerably higher in the unsuitable locations than in the suitable locations then it may be an important factor preventing the animal from inhabiting the unsuitable regions. The altitudinal range of the gelada baboon, for example, was found to be restricted by feeding time, which is likely to be the result of lower quality forage at altitudes above and below its current distribution (Dunbar 1992a). A study of baboons also found that feeding time is the key constraint on their distribution patterns (Bettridge et al. 2010). In contrast, studies looking at chimpanzees and gorillas using time budget models found that moving time (Lehmann et al. 2008b), body mass and predation (Lehmann and Dunbar 2009) all acted to restrict the ranges of these species. A model focussing only on the gorilla found that it was resting time that

prevented them from ranging more widely; this is probably related to their diet, which relies heavily on leaves as a fallback food (Lehmann et al. 2008a). Evidently, this approach can provide useful information about distribution patterns and the variables that have the strongest impact in determining habitat suitability. As deforestation and human encroachment continue to destroy orangutan habitat, it will become increasingly important to identify the factors that affect habitat suitability for the orangutan. This should help to identify the regions in which the orangutan has the highest chance of survival.

2.1.4 Social organisation

Time budget models can also be used to investigate the factors that affect grouping patterns. Orangutans spend the majority of their time alone, which is unusual for a large primate (Galdikas 1985a, van Schaik 1999, Bastian et al. 2010). This seems likely to be a response to harsh conditions that make grouping too expensive a strategy (Sugardjito et al. 1987, van Schaik and van Hooff 1996, van Schaik 1999). This is because fruit is patchily distributed in both space and time (Knott and Kahlenberg 2007), in small clumps relative to the size of an orangutan (Rodman 1977). Expressing low levels of association therefore appears to be a beneficial strategy to reduce the costs associated with feeding competition (Sugardjito et al. 1987). Through its effects on competition, grouping is therefore expected to have important consequences on an animal's time budget components. This has been observed at Tanjung Puting, where Galdikas (1988) found that socialising led to an increase in the focal animal's active day length, day range and time spent both moving and resting. A study focussing on groups formed at fig trees in Ketambe found that as aggregation size increased, individuals fed more and

rested less (Utami et al. 1997). Thus, orangutan time budget allocations appear to be affected by changes in social group size.

It is important to identify the time budget components that are most strongly affected by a rise in group size in the orangutan, as this may provide further evidence as to why orangutans have adopted an individual-based fission-fusion social system rather than living in larger, more stable groups. If indeed this is a result of ecological constraints, identifying the behaviours that are most affected by group size will help us to understand the mechanism underlying this and the precise element of the orangutan's ecology that makes grouping so costly. Time budget models have been used to show that both spider monkeys and chimpanzees considerably reduce their moving time requirements by adopting a fission-fusion social system (Korstjens et al. 2006, Lehmann et al. 2007a). Group size among great apes has been found to be critically dependent upon body mass, with the larger bodied gorillas living in smaller groups (Lehmann and Dunbar 2009). The fission-fusion strategy adopted by chimpanzees is thought to provide small benefits to the larger gorillas, which may help to explain why gorillas have not adopted this behavioural strategy (Lehmann and Dunbar 2009). Similarly, a time budget model indicated that black-and-white colobus monkeys may live in smaller groups than red colobus monkeys as a result of differences in resting time allocations. The results suggest that black-and-white colobus monkeys could live in similar sized groups to red colobus monkeys if their resting time component was less constrained by leaf feeding (Korstjens and Dunbar 2007). Time budget models can clearly provide a range of insights into primate grouping patterns.

Finally, it is also vital for orangutan conservation to identify the regions where they have the greatest chance of survival into the future, as well as the areas where they are most vulnerable. This can be achieved by looking at the areas where the orangutan

experiences the least constraints in terms of time; i.e. where they have excess time each day once all activities essential for survival have been performed. If habitat degradation occurs, orangutans may need to spend additional time performing their essential behaviours; for example, deforestation may lead to a reduction in the availability of food and so orangutans may need to spend more time moving in order to find enough food, which in turn increases their energetic requirements. Where orangutans have excess time available each day, this can be allocated to fulfil these additional demands; however, where orangutans are already at the limits of their time budget, they will have no flexibility to respond and so will be extremely vulnerable to any further habitat degradation that occurs.

2.1.5 Anthropogenic effects

2.1.5.1 Hunting

In any investigation of the current range of the orangutan, it is essential to remember that human factors have played an important role in limiting distribution patterns in the past, and that these pressures have intensified in recent years (Rijksen and Meijaard 1999). Despite the protected status of the orangutan in both Malaysia and Indonesia, hunting by local people continues (Rijksen and Meijaard 1999, Marshall et al. 2006). Recent human population growth in South-east Asia has been extremely rapid (Lane 2010) leading to increased hunting pressures on orangutans (Sodhi et al. 2004).

Orangutans have extremely slow reproductive rates, producing offspring only every nine years on average (Wich et al. 2009). Populations experiencing no external threats therefore only grow at a rate of two percent annually (Marshall et al. 2009). This means that hunting can rapidly drive orangutan populations to extinction. A population viability analysis has been used to show that in the best quality habitats, a hunting rate

of one percent can be sustainable, but that a rate of two or three percent would quickly lead to extinction (Marshall et al. 2009). Hunting has also been shown to have a negative effect on orangutan densities in East Kalimantan, where densities were positively correlated with the distance from the nearest village in which hunting was practised (Marshall et al. 2006). Surveys conducted in villages in Kalimantan indicated that between 750 and 1800 orangutans were killed between 2008 and 2009 in this region; even the lower estimate is not sustainable in the long-term (Meijaard et al. 2011). Thus, hunting by humans, both historically and in contemporary South-east Asia, exerts a considerable impact on the orangutan's distribution patterns and survival chances.

2.1.5.2 The effect of land cover change on the orangutan

Land cover change has played an important role in reducing the distribution of the orangutan. There is evidence that populations have declined by 95% in the last few centuries, and that this is largely attributable to recent habitat changes (Goossens et al. 2006). Deforestation has a number of important negative effects on both the forests and the orangutans that inhabit them. There is evidence from a number of studies indicating that logging has negative effects on orangutan densities. Husson et al. (2009), for example, found that across Bornean sites, logged forests have lower densities than unlogged forests. Disturbed peat and lowland forests in Gunung Palung had lower densities of orangutans than comparable primary forest (Johnson et al. 2005). At Sabangau, a peat-swamp forest in Borneo, orangutan density decreased following disturbance (Morrogh-Bernard et al. 2003), and densities in a logged forest in Sabah were lower than those in nearby primary forest (Davies 1986). In a selectively hand-logged forest in West Kalimantan, orangutan densities were 21% lower than in a

comparable unlogged forest. The logged forest also had fewer large food trees, and more canopy gaps (Felton et al. 2003), which may help to explain the lower densities. Similarly, at Ketambe in Sumatra, both orangutan densities and the availability of ripe fruit in a logged forest were only 40% of those in an unlogged forest (van Schaik and Rao 1997).

In contrast to these findings, some studies have shown that orangutans are able to subsist at relatively high densities in fragmented (Ancrenaz et al. 2004), selectively logged areas and logged areas (Russon et al. 2001). However, it should not be assumed that the negative effects of logging will be immediately apparent, as species may take many years to decline in response to altered conditions. These populations may therefore represent those destined for extinction. In addition, it is important to mention that a number of studies have reported very high densities of orangutans in forest neighbouring logging concessions; however, this is likely to be a result of overcrowding by orangutans fleeing from disturbances, and should not be interpreted as sustainable densities (Davies 1986, Husson et al. 2009). Nevertheless, if forests are able to regenerate, they can be a suitable habitat for orangutans. There is evidence that forest selectively or lightly logged in the past and allowed to recover to some extent can support densities that do not differ significantly from those in primary forest (Knop et al. 2004, Ancrenaz et al. 2010). Overall, however, logged forests appear to be inferior habitat to primary forest in that they can support fewer orangutans.

Deforestation has also been shown to alter behavioural patterns. A comparison between a logged and a primary forest at Ketambe showed that the two orangutans observed to enter the logged area spent more time moving and less time resting in this area than in the pristine forest. In addition, dietary changes were observed, with an increase in leaf eating in logged areas, compared to more fruit consumption in the primary forest (van

Schaik and Rao 1997). A later study at Ketambe found similar results, with significantly more time spent moving and a trend towards less time spent resting in logged areas than primary forest (Hardus et al. 2012). This is interpreted as a response to potentially more scattered food sources and fewer suitable resting sites in the logged forest.

In Borneo and Sumatra deforestation is commonly associated with subsequent conversion to plantations (Miettinen et al. 2011a), particularly oil palm which is currently one of the most lucrative cash crops (Nantha and Tisdell 2009, Tan et al. 2009). Although it has been shown that plantations can support a surprising amount of biodiversity (Koh and Gardner 2010), faunal species in oil palm plantations are often generalists of low conservation concern (Danielsen et al. 2009). Oil palm plantations support even fewer species than most other agricultural plantations (Fitzherbert et al. 2008). Orangutans living in close proximity to oil palm plantations expressed low levels of crop-raiding and ranging within these plantations, indicating that they provide few, if any, benefits to orangutans (Campbell-Smith et al. 2011b). There are also reports of orangutans in plantations being killed both for meat and to protect the crops (Tan et al. 2009). Orangutans have been found in acacia plantations, but the long-term viability of this population has yet to be determined (Meijaard et al. 2010a). Plantations can therefore not be considered to be particularly suitable habitat for orangutans, though they may be able to subsist in some forms of plantations if they also have access to areas of primary rainforest (Meijaard et al. 2010a, Campbell-Smith et al. 2011b).

Recent land cover changes have had an important effect on orangutans, altering their distribution, densities and behaviour. Much of this land conversion has occurred relatively recently, in many areas that are assumed to be climatically suitable for the

orangutan based on past distribution patterns. It is therefore important to consider the impact of land cover changes in any investigation of orangutan distribution patterns.

2.1.6 Chapter aims

1. To investigate predicted time budget allocations across Borneo and Sumatra, to determine the factors that restrict the current range of the orangutan.
2. To determine the effect of group size on time budget components. This will shed light on the factors that contribute to the largely solitary nature of the orangutan.
3. To explore the distribution of maximum ecologically tolerable group sizes within the current range of the orangutan. This will identify the relative levels of time budgeting stress faced by the orangutan in different regions of its range, and consequently its vulnerability to future habitat change.

2.2 Methods

2.2.1 Data collection

Data were collected from published studies to compile a dataset of orangutan time budgets (time spent feeding, moving and resting), diet (percentage of feeding time spent eating fruit and leaves) and group size. Data were collected from 13 different orangutan study sites in total, nine in Borneo and four in Sumatra (Figure 2.1), with time budget data available for 12 of the sites (Table 2.1). Where data for more than one time period were available for a site, average values were used so that each site was only represented once in the dataset.

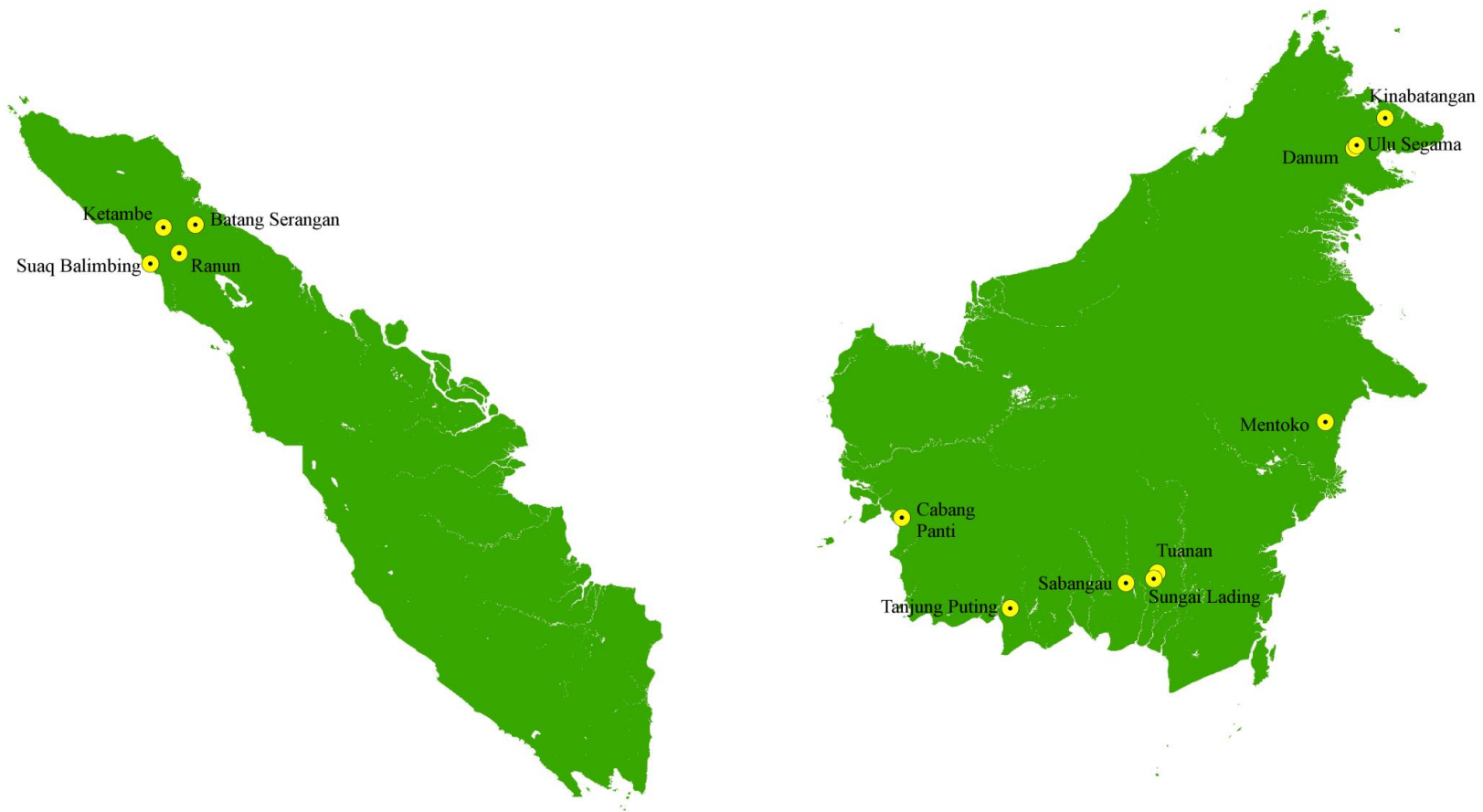


Figure 2.1: Locations of the sites in Sumatra and Borneo

Climate data were obtained from Worldclim (Hijmans et al. 2005) and are displayed in Table 2.2. Worldclim provides a set of global climate layers for 19 bioclimatic variables at a resolution of 30 arc seconds. These layers were generated through interpolation of average monthly climate data from weather stations across the world, from 1950-2000 (Hijmans et al., 2005). All 19 variables were used in the equation finding process. The percentage of forest cover data, displayed in Table 2.2, was obtained from the Advanced Very High Resolution Radiometer (AVHRR) satellite data (Defries et al. 2000). The forest cover value obtained for Suaq Balimbing, a field site in northern Sumatra, was 23%. This value was considerably lower than even that found for the heavily degraded site at Batang Serangan (Campbell-Smith et al. 2011b). Given that Suaq Balimbing is characterised by extremely high densities of orangutans, it seems likely that this is an anomalous data point, caused by inaccuracies in the forest cover dataset or the low resolution of the coordinates given for the site. The forest cover value for this site was therefore extracted from the MODIS dataset (Hansen et al. 2003), which gives a value of 80%. Although the MODIS dataset is from 2000 and so it is more recent than the AVHRR data, it was not chosen as an alternative for the overall model as it seems to overestimate forest cover in southern Sumatra (when compared with the AVHRR dataset and both the GLC2000 and the 2010 land cover maps). It seems likely that the MODIS data includes plantations as forest cover, leading to inflated values in some areas. High levels of forest cover under MODIS could therefore represent either dense plantations or dense primary forest cover. The difference between the two is likely to have a considerable effect on orangutan time budgets, and so it is important to be able to distinguish between them. Consequently, the AVHRR dataset was used as it seems to distinguish more accurately between plantations and primary forest cover; with plantations being represented by very low values and primary forest by high values.

Table 2.1: Orangutan study sites and their locations (latitude, longitude and island), with the species/subspecies studied and the behavioural data (group size, feeding, moving and resting time) and dietary data (% fruit and leaves in the diet) used in the equation finding process. Averages were used when data from more than one study were available for the same site, so that each site is only represented once in the dataset. Behavioural data were taken from:

¹ Kanamori et al. 2010; ² Morrogh-Bernard et al. 2009; ³ Rodman 1973, Rodman 1979, Mitani 1989, Mitani 1990; ⁴ Mackinnon 1974; ⁵ Morrogh-Bernard et al. 2009; ⁶ Mitani et al. 1991, van Schaik 1999, Morrogh-Bernard et al. 2009; ⁷ Galdikas 1984, Galdikas 1988; ⁸ Morrogh-Bernard et al. 2009, Bastian et al. 2010; ⁹ Bastian et al. 2010; ¹⁰ Campbell-Smith 2010; Campbell-Smith et al. 2011b, ¹¹ Sugardjito et al. 1987, van Schaik 1999, Wich et al. 2006; ¹² Mackinnon 1974; ¹³ van Schaik 1999, Fox et al. 2004

Site	Latitude	Longitude	Island	Species/subspecies	Group Size	%Feeding	%Moving	%Resting	%Fruit	%Leaves
Danum ¹	5.02	117.75	Borneo	<i>P. pygmaeus morio</i>	-	47.2	16.9	34.4	60.9	22.2
Kinabatangan ²	5.53	118.28	Borneo	<i>P. pygmaeus morio</i>	-	34.1	10.3	53.6	68.0	22.9
Mentoko ³	0.40	117.27	Borneo	<i>P. pygmaeus morio</i>	1.28	45.2	10.4	43.1	53.8	29.0
Ulu Segama ⁴	5.07	117.80	Borneo	<i>P. pygmaeus morio</i>	1.93	32.3	16.4	51.4	51.5	-
Sabangau ⁵	-2.32	113.90	Borneo	<i>P. pygmaeus wurmbii</i>	-	61.3	15.9	19.7	73.8	5.1
Cabang Panti ⁶	-1.22	110.12	Borneo	<i>P. pygmaeus wurmbii</i>	1.04	36.1	9.9	52.8	70.0	13.4
Tanjung Puting ⁷	-2.75	111.95	Borneo	<i>P. pygmaeus wurmbii</i>	1.18	60.1	18.7	18.2	60.9	14.7
Tuanan ⁸	-2.15	114.43	Borneo	<i>P. pygmaeus wurmbii</i>	1.13	50.6	16.8	30.9	69.8	17.2
Sungai Lading ⁹	-2.25	114.37	Borneo	<i>P. pygmaeus wurmbii</i>	1.03	-	-	-	61.0	-
Batang Seragan ¹⁰	3.73	98.19	Sumatra	<i>P. abelii</i>	-	24.0	15.0	54.0	46.0	13.0
Ketambe ¹¹	3.68	97.65	Sumatra	<i>P. abelii</i>	2.04	48.2	12.8	38.8	62.8	20.8
Ranun ¹²	3.25	97.92	Sumatra	<i>P. abelii</i>	1.85	44.1	16.0	40.0	84.7	10.2
Suaq Balimbing ¹³	3.07	97.43	Sumatra	<i>P. abelii</i>	1.90	53.1	17.3	27.2	66.2	15.5

Table 2.2: Forest cover and climate data (temperature variables are in °C and precipitation variables are in mm)

T_a = annual mean temperature; T_d = mean temperature diurnal range (mean of monthly max temp - min temp); T_i = isothermality ((mean diurnal range/temperature annual range) * 100); T_s = temperature seasonality (standard deviation *100); T_x = maximum temperature of warmest month; T_m = minimum temperature of coldest month; T_r = temperature annual range (maximum temperature of warmest month - minimum temperature of coldest month); T_{we} = mean temperature of wettest quarter; T_{dr} = mean temperature of driest quarter; T_{wa} = mean temperature of warmest quarter; T_c = mean temperature of coldest quarter; P_a = annual precipitation; P_w = precipitation of wettest month; P_d = precipitation of driest month; P_s = precipitation seasonality (coefficient of variation); P_{we} = precipitation of wettest quarter; P_{dr} = precipitation of driest quarter; P_{wa} = precipitation of warmest quarter; P_c = precipitation of coldest quarter

Bioclim Variables																				
Site	Forest cover (%)	T_a	T_d	T_i	T_s	T_x	T_m	T_r	T_{we}	T_{dr}	T_{wa}	T_c	P_a	P_w	P_d	P_s	P_{we}	P_{dr}	P_{wa}	P_c
Danum	80	26.1	7.6	8.7	36.4	30.7	22.0	8.7	25.7	25.9	26.5	25.5	2386	264	146	15	718	523	523	698
Kinabatangan	64	27.0	7.9	8.5	46.8	32.0	22.8	9.2	26.3	27.3	27.5	26.3	2711	362	131	31	977	479	479	977
Mentoko	80	26.1	7.0	8.8	23.7	30.2	22.3	7.9	26.2	25.9	26.3	25.9	1973	228	102	27	645	325	543	363
Ulu Segama	72	26.3	7.7	8.7	37.1	31.0	22.2	8.8	25.9	26.5	26.7	25.7	2416	275	143	17	742	516	516	727
Sabangau	79	26.6	8.2	8.6	36.8	31.8	22.3	9.5	26.1	26.9	27.0	26.1	2579	294	123	29	836	395	434	812
Cabang Panti	52	25.3	8.6	9.1	31.0	30.2	20.8	9.4	24.8	25.4	25.5	24.8	3258	364	134	27	1069	495	787	1069
Tanjung Puting	80	26.8	8.2	8.7	35.9	31.9	22.5	9.4	26.9	27.0	27.1	26.2	2723	295	148	22	824	471	506	783
Tuanan	80	26.6	8.1	8.7	30.5	31.6	22.3	9.3	26.2	26.8	26.9	26.2	2522	285	108	32	837	366	399	837
Sungai Lading	80	26.6	8.1	8.4	35.0	31.8	22.2	9.6	26.2	26.8	27.0	26.1	2508	285	109	33	841	364	398	838
Batang Seragan	33	26.8	9.6	8.7	43.1	32.5	21.5	11.0	26.5	26.5	27.3	26.2	2608	311	123	26	862	465	623	720
Ketambe	80	24.8	9.8	8.8	38.4	30.6	19.5	11.1	24.4	24.9	25.3	24.3	2563	298	123	27	871	440	626	763
Ranun	69	24.4	9.9	8.8	38.0	30.2	19.0	11.2	24.0	24.4	24.9	23.9	2868	331	138	26	956	500	787	852
Suaq Balimbing	80	26.9	9.5	8.7	43.7	32.6	21.8	10.8	26.5	27.0	27.5	26.3	2950	344	158	25	953	559	716	821

2.2.2 Model Components

The main components of the model were diet, group size and time budgets. In addition, anthropogenic effects were included, as present day primate distributions are heavily affected by human activities, such as land cover change and human population densities, which are not reflected in the climate data.

2.2.2.1 Diet

The orangutan diet is composed mainly of fruit and leaves (Morrogh-Bernard et al. 2009, Russon et al. 2009), which make up more than 80% of their feeding time (see Table 2.1), thus only these two food categories were included in the model. These variables were measured as the percentage of feeding time spent consuming fruit and leaves, which were assumed to be mutually exclusive. Diet was assumed to be influenced by the climate and the percentage of forest cover.

2.2.2.2 Group size

Orangutans are characterised by an individual-based fission-fusion social system (van Schaik 1999) which makes the definition of group utilised in previous time budget models for other species problematic. In the previous models, the group is defined as ‘the relatively stable set of individuals who share a common range’ (Lehmann et al. 2010a). This definition does not transfer well to the orangutan system in which individuals live in loose communities that are neither socially nor spatially exclusive (Singleton and van Schaik 2002) and spend a large proportion of their time alone (Galdikas 1981, van Schaik 1999, Bastian et al. 2010). Although females have been shown to associate preferentially with neighbouring individuals, forming loose clusters, these clusters are not exclusive and therefore can not be viewed as discrete social units.

Orangutans have large individual home ranges that overlap considerably with one another, but do not form a distinct community range (Singleton and van Schaik 2002, Morrogh-Bernard 2009). Thus, orangutans do not live in closed communities with a clearly defined membership, but have flexible social relationships with neighbouring individuals (Singleton et al. 2009, van Noordwijk et al. 2012). The group size as defined in previous studies is therefore not a relevant concept when looking at the orangutan social system. Orangutans, however, do form distinct parties, i.e. temporary aggregations. These parties are usually extremely small, composed of only a few individuals. The average party size of adult females found across the eight sites for which there were data was only 1.49 independent individuals. Among orangutans it appears to be the party that is the key social unit, in which individuals feed, travel and socialise together. Therefore, it is expected that the size of this unit will be an important determinant of time budget allocations, and ultimately of the range of environments in which they can survive. Thus, group size will refer to party size in the orangutan time budget model. Party size among orangutans is usually measured as the average party size of adult females, excluding dependent individuals (van Schaik 1999).

2.2.2.3 Time budgets

Feeding, moving and resting time allocations were assumed to be affected by the climate, percentage forest cover, diet and group size. As orangutans form relationships with neighbouring individuals (Singleton and van Schaik 2002), grooming time was also included in the model, as grooming is seen as an activity that bonds individuals together. Grooming time was estimated from a generic equation calculated by Lehmann et al. (2007b) that determines the amount of time that individuals ought to devote to grooming to maintain group cohesion in a group of a particular size. This equation is

based on the observation that among primates grooming time increases as group size increases, a result of the increased time required for maintaining relationships and group cohesion (Lehmann et al. 2007b).

Bivariate Pearson correlation analyses, together with visual screening of the data, were used to identify possible linear and curvilinear relationships between the behavioural and dietary variables (Table 2.1) and the climate and forest cover data (Table 2.2). Forward stepwise multiple regression analyses were then performed to obtain best-fit equations to predict the percentage of fruit in the diet, feeding, moving and resting time, using the 19 climate variables, diet and group size as possible predictor variables. Variables were only added to an equation if their inclusion could be justified using biological first principles, and if they explained a significant proportion of the variation (Dunbar 1992b). Because of the small sample size, a maximum of three predictor variables were included in the regression equations (Korstjens and Dunbar 2007); the three variables that explained the highest proportion of the variance were selected. The predictions of the equations were constrained to within biologically realistic values, to prevent the model from producing mathematically possible, but biologically improbable results (Willems and Hill 2009). Feeding and resting time budget allocations were constrained to a minimum value of 10% and moving time was constrained to a minimum of 5%. The percentage of time that orangutans spend feeding on fruit and leaves was constrained to values between 0 and 100.

2.2.2.4 Anthropogenic factors

In addition to these core model components, anthropogenic effects were included. In the past century the total human population of Borneo and Sumatra has increased dramatically (Hirschman 1994), leading to intense deforestation and hunting pressures

(Sodhi et al. 2004). Although the percentage of forest cover, an indication of deforestation, was included in the model, the data were based on satellite imagery collected in 1992-1993 and are therefore unlikely to be representative of the current situation, especially given the extremely rapid rate of deforestation in Borneo and Sumatra - forest cover declined by 1.3% in Borneo and 2.7% in Sumatra per year between 2000 and 2010 (Miettinen et al. 2011a). In order to account for the increasing impact of anthropogenic factors on the orangutans, a recent land cover map from 2010 was incorporated into the model (Miettinen et al. 2011b), so that areas where human induced land use changes are likely to prevent orangutans from persisting could be identified. Land cover categories were classified as those suitable and unsuitable for orangutans (Table 2.3). Categories were classed as unsuitable if they were heavily logged, agricultural land or open areas, while forested areas were classed as suitable habitat.

Table 2.3: Land cover categories from the 2010 land cover map (Miettinen et al. 2011b)

Suitable Habitat
<ul style="list-style-type: none"> ▪ Mangrove ▪ Peatswamp forest – forest growing on peat soil ▪ Lowland forest – forest growing on mineral soil up to altitudes of 750m above sea level ▪ Lower montane forest - forest growing on mineral soil between altitudes of 750m-1500m above sea level ▪ Upper montane forest - forest growing on mineral soil at altitudes above 1500m above sea level
Unsuitable habitat
<ul style="list-style-type: none"> ▪ Plantation/regrowth – includes young secondary forests and heavily logged forests dominated by regrowth ▪ Lowland mosaic - typically consists of small plantations, agricultural fields, urban areas, and patches of forest and secondary forest ▪ Montane mosaic - similar to lowland mosaic, but at altitudes above 750m ▪ Lowland open - typically agricultural and heavily degraded areas up to 750m ▪ Montane open - similar to lowland open, but at altitudes above 750m, and includes some naturally bare areas at high elevations ▪ Urban – major urban areas ▪ Large-scale palm plantation

Human population density (HPD) was also added to the model as it can be used as a summary measure of human impacts, such as hunting pressures (Cardillo et al. 2004). HPD data were obtained from the Oak Ridge National Laboratory LandScan 2008™ High Resolution Global Population Data Set (Bright et al. 2009). In order to choose an appropriate threshold for the value of HPD, above which orangutans were unlikely to survive, the distribution of HPD values within locations in the observed orangutan range was examined. Although some locations within the orangutan range have extremely high values of HPD, this is likely to be the result of errors in estimation of either HPD or the orangutan range. A threshold of 20 people per square kilometre was chosen as an appropriate threshold as almost 97% of locations within the orangutan range were

characterised by HPD values lower than this threshold (Table 2.4). In addition, increasing the threshold above 20 people per square kilometre leads to relatively small increases in the percentage of locations with HPD values below the threshold, while decreasing the threshold below 20 leads to increasingly large decreases in this percentage. This indicates that orangutans may struggle to survive in locations with HPDs above 20 people per square kilometre.

Table 2.4: The proportion of the current orangutan range with human population densities below different thresholds

Threshold value of HPD (people per km ²)	Proportion of orangutan range with HPD < threshold
30	97.7
25	97.3
20	96.8
15	95.2
10	92.7
5	86.3

2.2.3 Model Procedure

The equations were implemented in ArcGIS version 9.3 (ESRI 2008) using the raster calculator function to predict time budget allocations of orangutans for each pixel in a raster image across Borneo and Sumatra. The maximum ecologically tolerable group size was determined by calculating the sum of the time budget allocations for each pixel. Group size was then increased algorithmically from one, until the total time budget allocations exceeded 100%. The maximum ecologically tolerable group size is defined as the group size of the previous iteration. In order for orangutans to survive in a location, they must be able to live in a group size between the ecological maximum and minimum (which in primates is generally determined largely by predation risk). Orangutans are not considered to face high predation risk (van Schaik and van Hooft

1996); indeed, orangutans spend the majority of their time alone (Galdikas 1985a, van Schaik 1999, Bastian et al. 2010) and have been observed to live in average group sizes as low as 1.03 and 1.04 at Sungai Lading and Cabang Panti respectively (Mitani et al. 1991, Bastian et al. 2010). The minimum group size for orangutan survival is therefore assumed to be one. Thus, the orangutan is predicted to be able to survive in all pixels with a predicted maximum ecologically tolerable group size greater than or equal to one, a suitable land cover category and a HPD value less than 20 people per square kilometre.

2.2.4 Validating the model

The model was validated in three ways. Firstly, the predicted distribution was compared against the observed range of the orangutan, to determine how accurately the model predicted the current distribution. The observed distribution was obtained from UNEP-WCMC and was based on extensive ground and aerial surveys and forest data from both satellite imagery and the Indonesian Ministry of Forestry (Meijaard et al. 2004, Wich et al. 2008). Secondly, predicted values for orangutan maximum ecologically tolerable group size were compared with observed values from the nine sites for which there were data. Observed group sizes should be equal to or less than predicted maximum values. The difference between observed and predicted group sizes was analysed using Wilcoxon signed-ranks tests in SPSS (SPSS 2008). Finally, sensitivity analyses were used to evaluate the robustness of the model to errors in parameter estimates. The parameter estimates in the regression equations were each changed one at a time by +5%, -5%, +50% or -50% and the model re-run. All parameters were then changed simultaneously by +5%, -5%, +50% or -50% and the four resulting models run. The predictions of the altered models were compared to the predictions of the original model

to determine the sensitivity of the model to error. Ideally, the model should be robust to small changes in parameter estimates (~5%) but sensitive to large changes (~50%). Comparing spatial data can be problematic, as the data often violate the assumptions of statistical tests. The outputs from the sensitivity analysis were therefore compared with the original model predictions using two different methods, to ensure that the results were reliable.

One of the main problems with spatial data is that points that are in close proximity can not be considered to be independent. The first method therefore involved the creation of a grid consisting of 374 locations across Borneo and Sumatra separated by 0.5° longitude and latitude. The prediction (i.e. presence or absence) at each of these grid locations was extracted for the original model and all sensitivity analysis models for comparison. This improved the independence of the data compared to pixel level resolution and thereby allowed the predictions of the altered models to be compared with those of the original model. Chi-squared tests were used to determine if the altered equations produced significantly different results from the original model. These analyses were performed in SPSS version 17 (SPSS 2008).

The second method involved calculating the percentage agreement between the sensitivity analyses output rasters and the original model output. The percentage agreement should be high for small changes of only 5%, and lower for changes of 50%. This was performed using IDRISI Taiga (Eastman 2009).

2.2.5 Constraints on biogeography and sociality

Mean time budget allocations were compared between the sites where the orangutans were correctly predicted to be present, and those where they were correctly predicted to be absent to determine the factors that restrict biogeography. As resting and social time

are influenced by the group size, a constant group size of one was used in all these comparisons. In order to test the significance of the differences and avoid problems with dependent data, values were extracted from the points on the grid, each separated by 0.5° longitude and latitude, as this improves the independence of the data. These values were not normally distributed and so were compared using Mann-Whitney U tests in SPSS (SPSS 2008). Finally, the maximum ecologically tolerable group size predicted across the range of the orangutan was examined.

2.3 Results

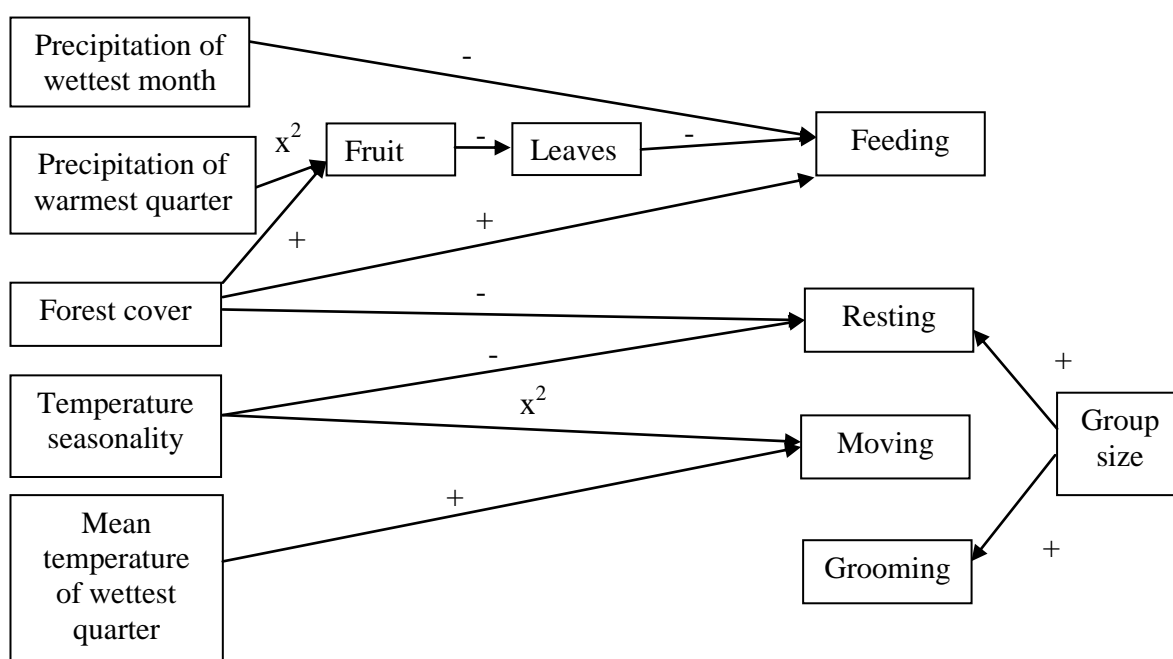
2.3.1 Equations

The regression equations obtained are presented in Table 2.5 and summarised in Figure 2.2. In addition to the equations for feeding, moving and resting time, a regression equation was produced for the percentage of fruit in the diet from which the percentage of leaves in the diet can be calculated, as this variable was a significant predictor of feeding time.

Table 2.5: Multiple regression equations for time budget and diet variables

Variable	Equation	R^2_{adj}	N	F	P
Feeding	$22.081 + 0.665*Forest - 0.806*Leaves - 0.032*Precipitation\ of\ Wettest\ Month$	0.91	11	35.99	<0.001
Moving	$-97.085 + 0.358*Temperature\ Seasonality - 0.0005*Temperature\ Seasonality^2 + 0.189*Mean\ Temperature\ of\ Wettest\ Quarter$	0.56	12	5.61	<0.01
Resting	$128.548 + 27.417*Group\ size - 0.968*Forest - 0.176*Temperature\ Seasonality$	0.88	8	17.58	<0.05
Fruit	$174.100 - 0.488*Precipitation\ of\ Warmest\ Quarter + 0.0004*Precipitation\ of\ Warmest\ Quarter^2 + 0.267*Forest$	0.56	13	6.06	<0.05
Leaves	$100 - \%Fruit$				
Grooming	$1.01 + 0.23*Group\ size$	Generic equation†			

† Equation from (Lehmann et al. 2007b)

**Figure 2.2:** Flow chart depicting relationships between climate and forest cover variables and the time budget components. The arrows indicate directional relationships used in the model, + indicates a positive relationship, - a negative relationship and x^2 a quadratic relationship.

Predicted values for feeding, moving, resting and the percentage of fruit in the diet are very similar to the observed values, giving confidence in the ability of the equations to accurately predict time budget allocations (Table 2.6). The prediction for grooming time can not be compared to observed data, as orangutans are in fact very rarely observed grooming (Galdikas 1995) and so data on grooming time were not available. However, orangutans do perform other social behaviours such as mating and play (Fox et al. 2004). The equation focusses on grooming time as it is a generic primate equation and in other primates, this is the most common social behaviour and is thought to be the key behaviour for social bonding (Lehmann et al. 2007b). However, in orangutans where grooming is rare, other social behaviours may play a more important role than in species that regularly groom one another. Social activities comprise a very small percentage of daily activity budgets and so are often included as other activities. Only two sites provided data for the time spent in other activities, including social behaviour; Danum = 1.5% (Kanamori et al. 2010) and Suaq Balimbing = 1% (Fox et al. 2004). The predicted values for grooming time ranged between 1.25 and 1.45 with a mean of 1.35. These values therefore seem to be realistic estimates for social time in orangutans.

Table 2.6: Observed mean and range for the time budget variables at the sites used in the equation finding process, with the equivalent values predicted by the equations

	Observed		Predicted	
	Mean	Range	Mean	Range
Feeding	44.7	24-61.3	45.8	23.6-61.1
Moving	14.7	9.9-18.7	13.9	9.2-17.8
Resting	38.7	18.2-54	37.9	20.3-52.2
Fruit	63.8	46-84.7	51.8	34.1-64.6

The equations highlight the important effect of forest cover on time budget allocations, as forest cover was an important predictor of feeding time, resting time and the percentage of fruit in the diet. The positive relationship between forest cover and fruit could be the result of a higher availability of fruit in dense forest than in more degraded habitats (van Schaik and Rao 1997). Forest cover also predicted feeding and resting time, and it is likely that these relationships are a result of the effect of forest cover on diet. In densely forested areas, orangutans may need to spend less time resting and more time feeding, possibly as a result of the increased availability of high quality food that requires less time for digestion but more time for extraction (which would be attributed to feeding time). Indeed, many orangutan fruits have been shown to require considerable extraction time (Leighton 1993, Knott 1998). In contrast, in more sparsely forested areas, orangutans may be forced to rest more to conserve energy (and to digest the higher percentage of leaves in their diet) and feed less. In addition, low forest cover will mean that orangutans are more exposed to the sun, which may force them to spend more time resting to avoid overheating (Pollard and Blumstein 2008). Resting time was also predicted by group size and temperature seasonality. As group size increases, fruit sources will be depleted faster and orangutans may be forced to consume more leaves which require more digestion time. The relationship with temperature seasonality indicates that orangutans spend more time resting in areas with more consistent temperatures. This may reflect higher resting time requirements in areas closer to the equator, where temperatures are more consistently high (Chuan 2005). When temperatures are high animals are unable to perform many of their essential activities, and are thus forced to rest (Korstjens et al. 2010).

Feeding time was negatively related to the amount of leaves in the diet, which by definition is negatively related to the amount of fruit in the diet. Similarly, among the

African apes, it was found that feeding time increased as the percentage of fruit in the diet increased (Lehmann et al. 2008b). These relationships may reflect the reduced foraging and processing times required to eat leaves.

Implementing these equations in ArcGIS 9.3 (ESRI 2008) produced raster images indicating the amount of time that orangutans ought to devote to each time budget component, as well as the percentage of fruit in the diet, across Borneo and Sumatra (Figures 2.3-2.7).

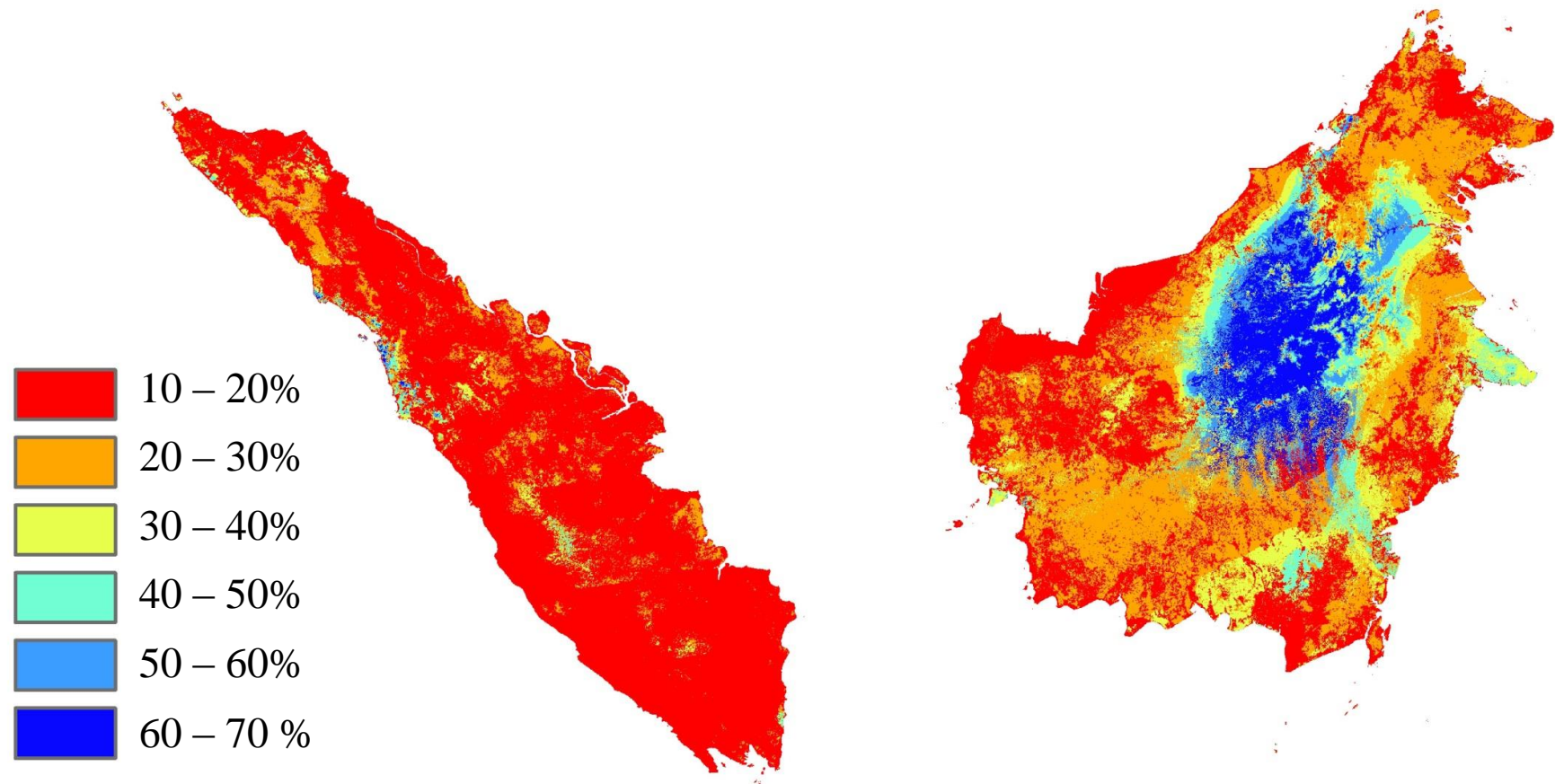


Figure 2.3: Predicted percentage of time spent feeding

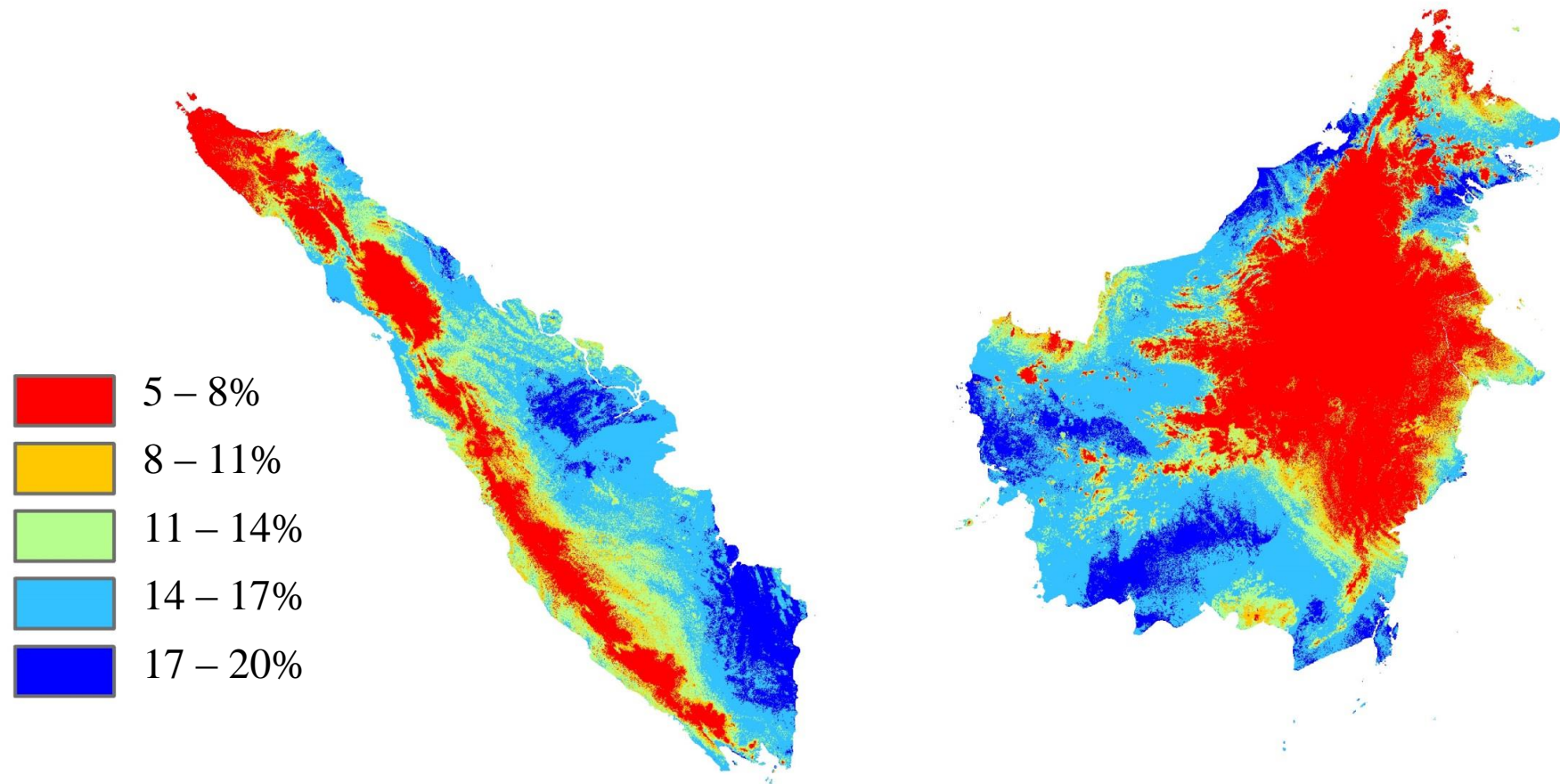


Figure 2.4: Predicted percentage of time spent moving

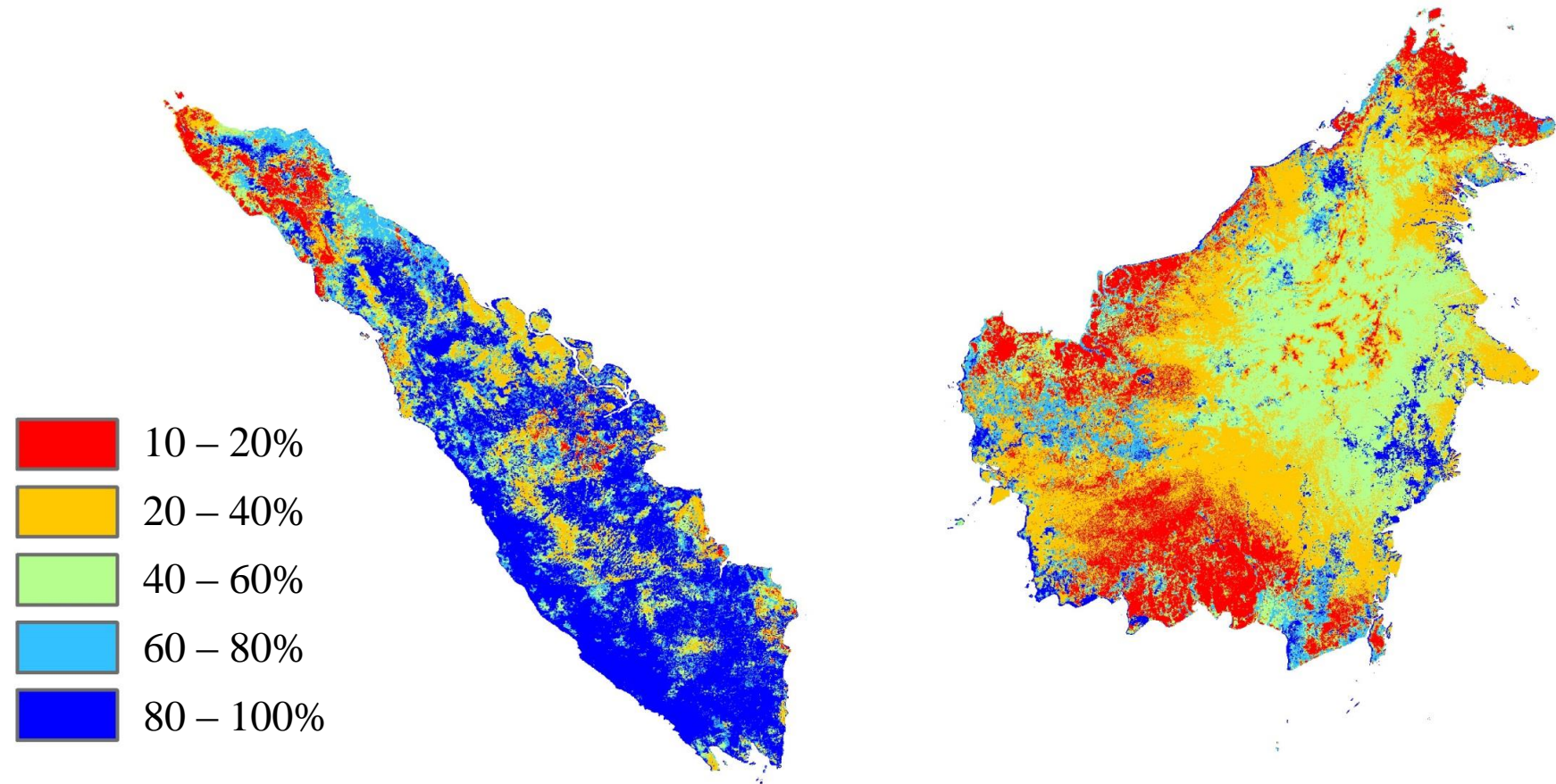


Figure 2.5: Predicted percentage of time spent resting

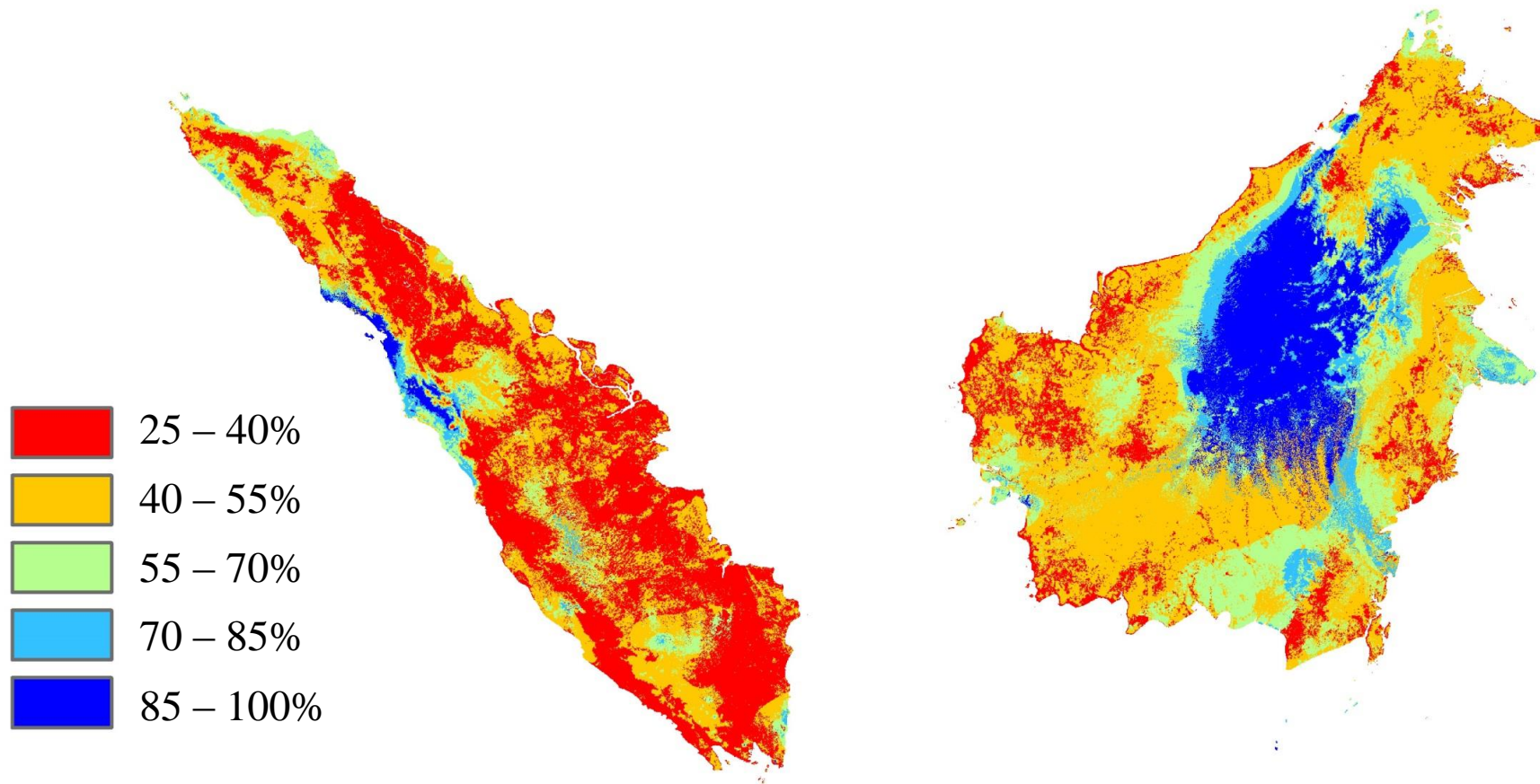


Figure 2.6: Predicted percentage of fruit in the diet

2.3.2 Model Validation

The current range of the orangutan is displayed in Figure 2.7. Figure 2.8 is the presence/absence map produced using the time budget equations alone and Figure 2.9 is the map produced by the full model, i.e. with the inclusion of the land cover and human population density filters. The presence/absence map produced by the full model was compared against the observed distribution, to produce a map indicating the areas where model predictions were correct, and those where they were false (Figure 2.10).

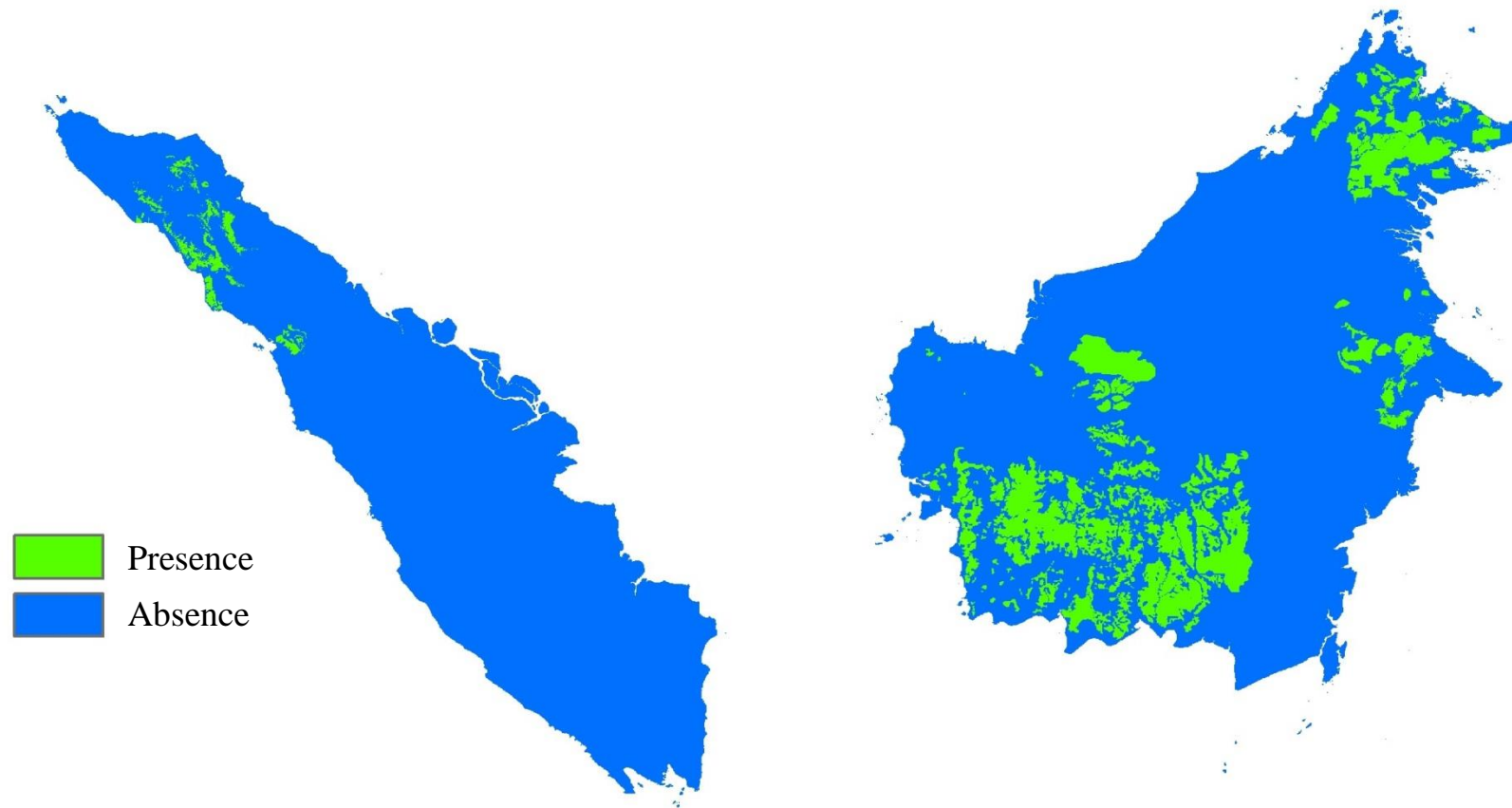


Figure 2.7: The current distribution of the orangutan (Wich et al. 2008)

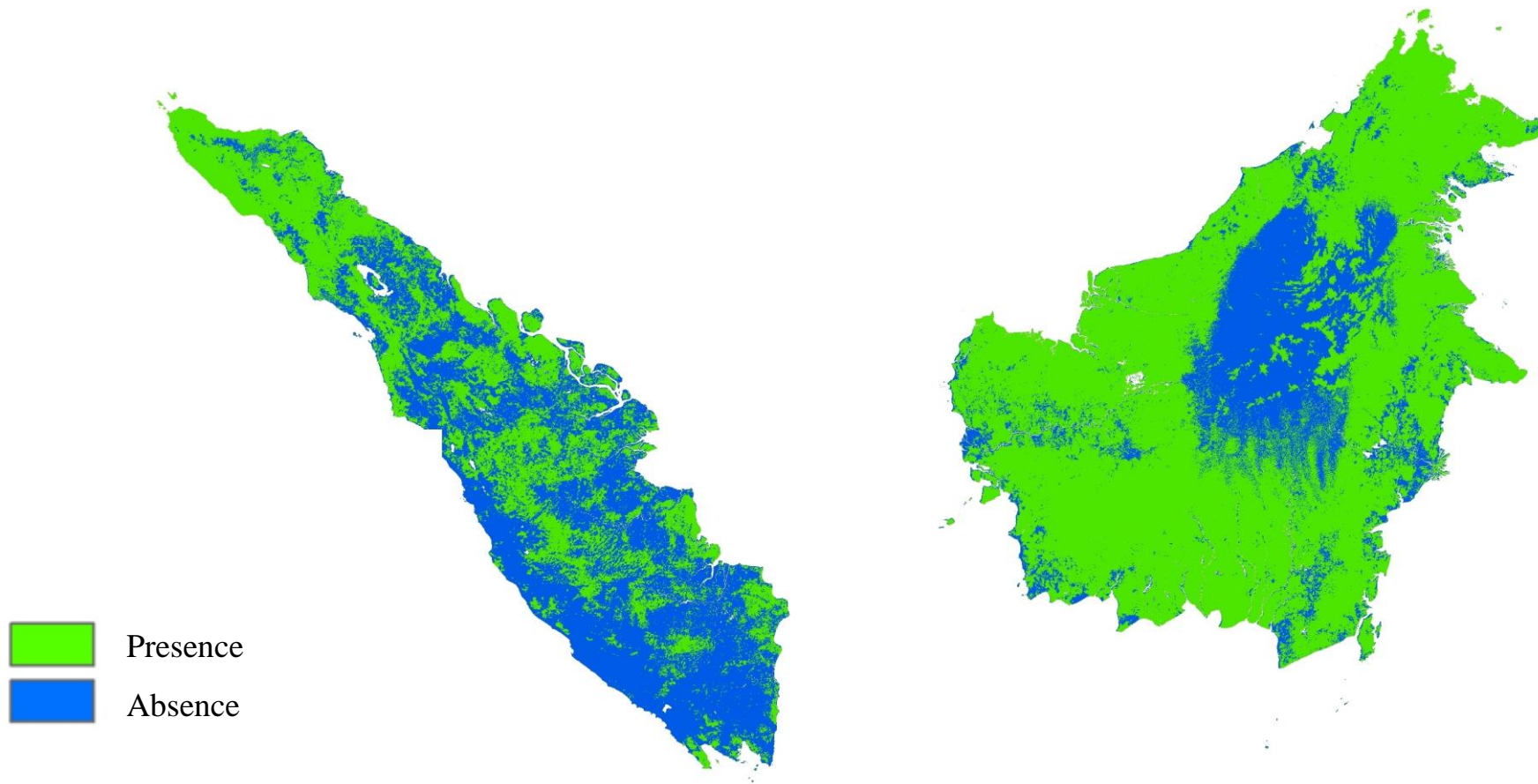


Figure 2.8: Predicted distribution of the orangutan using the time budget equations alone (excluding the land cover and human population density filters)

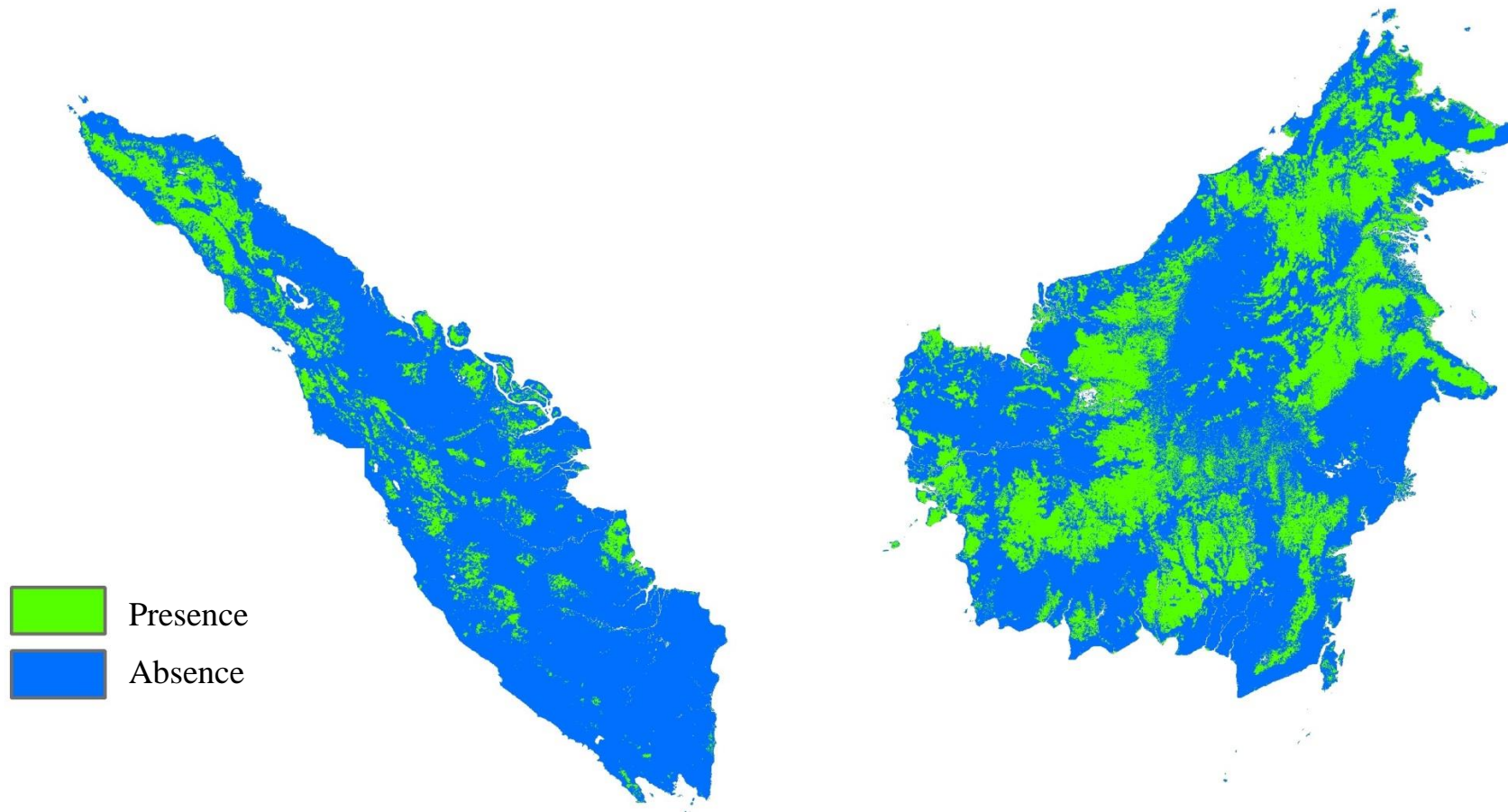


Figure 2.9: Predicted distribution of the orangutan using the full model (including the land cover and human population density filters)

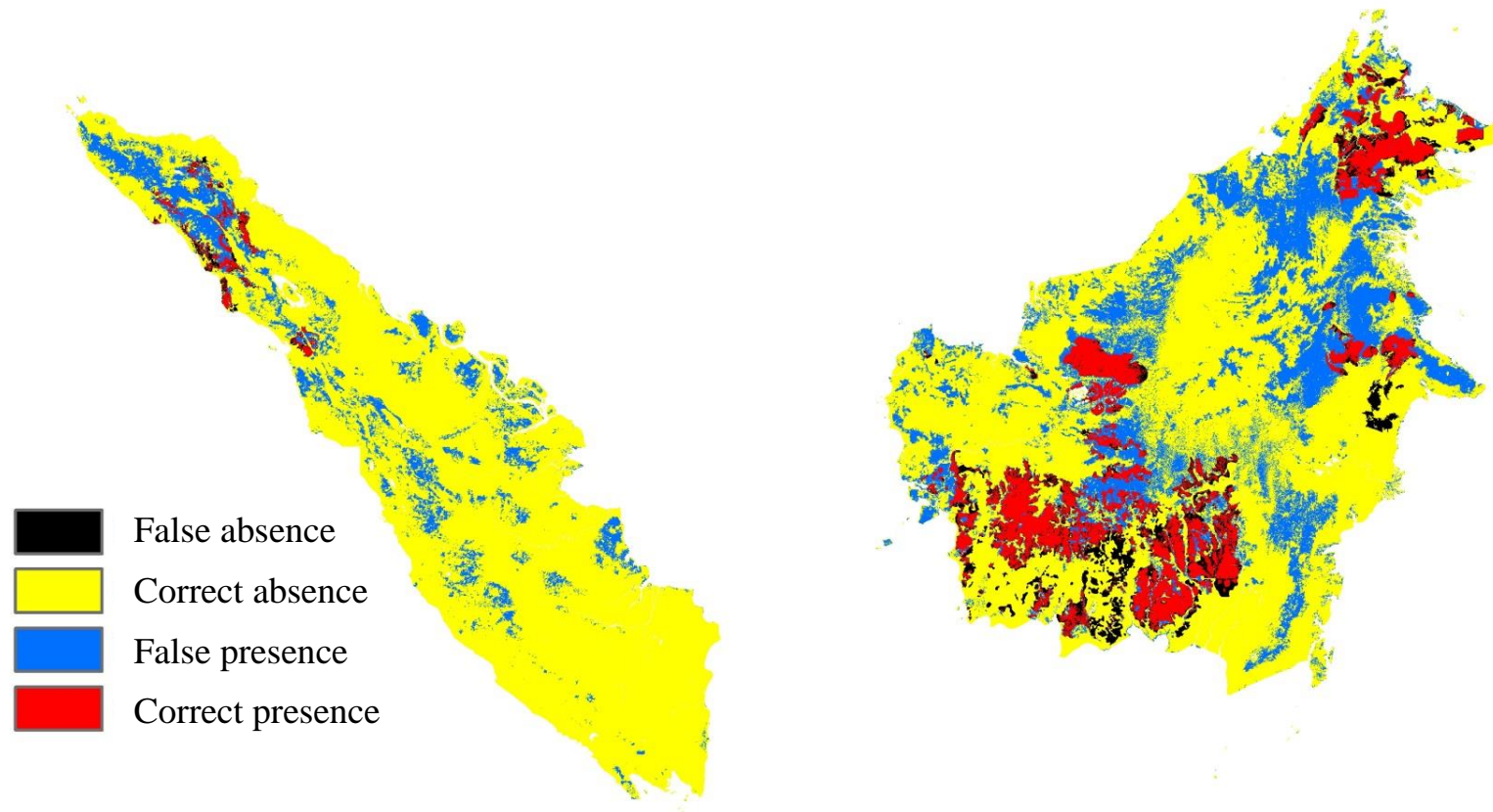


Figure 2.10: Predicted distribution of the orangutan based on the full model, compared against the observed distribution (false absences indicate locations where orangutans are present but the model predicted absence, correct absences are locations where orangutans are absent and the model predicted absence, false presences are locations where orangutans are absent and the model predicted presence and correct presences are locations where orangutans are present and the model predicted presence).

Overall, the basic time budget model correctly predicted the presence or absence of orangutans in 44.5% of raster pixels. The addition of the land cover and human population density data increased accuracy to 77.0%, highlighting the importance of anthropogenic factors in determining orangutan distribution patterns. The model correctly predicted orangutan absence from 78.1% of the areas from which they are currently thought to be absent and their presence in 68.3% of their current range (Table 2.7). The number of correct predictions (when analysed across the grid of 374 points) was significantly higher than would be expected by chance, based on the observed proportion of presences and absences ($\chi^2 = 11.87$, $df = 1$, $N = 374$, $P < 0.001$).

Table 2.7: Table of the performance of the time budget model (including both land cover and HPD filters), displaying the percentage of observed presences and absences that were predicted to be presences and absences

		Observed	
		Present	Absent
Predicted	Present	68.3	21.9
	Absent	31.7	78.1
Total		100	100

The model therefore incorrectly predicted the presence or absence of orangutans in just over 20% of raster pixels. The majority of these false predictions were those where the model predicted suitable habitat for orangutans but no orangutans were recorded to live there in 2007, i.e. the map overestimated the current orangutan range. An orangutan distribution map was obtained for the island of Borneo from 1930 (Rijksen and Meijaard 1999), and compared with the model predictions for Borneo. This showed that 45.2% of these false presences were in land that was inhabited by orangutans according to the 1930 map, thereby confirming that climatically these areas may indeed be suitable. Similarly, 58.3% of those locations that were incorrectly identified as unsuitable for orangutans by the model were in areas that were classified as plantations

or regrowth in the 2010 land cover map, and were thus classed as unsuitable for orangutans. This conversion to plantations appears to be relatively recent, as 75.2% of the locations classified as plantations in 2010 were classed as forested in a land cover map from 2000 (GLC 2003). Consequently, many of these areas may no longer be suitable for orangutan habitation.

Observed group sizes were compared against the maximum ecologically tolerable group sizes predicted by the model. Observed group sizes should be less than or equal to the maximum ecologically tolerable group size; Figure 2.11 shows that this was the case for all of the points. Predicted maximum ecologically tolerable group sizes were significantly higher than observed group sizes (WSR: $z = -2.668$, $N = 9$, $P < 0.01$), and still within a realistic range of the observed grouping patterns.

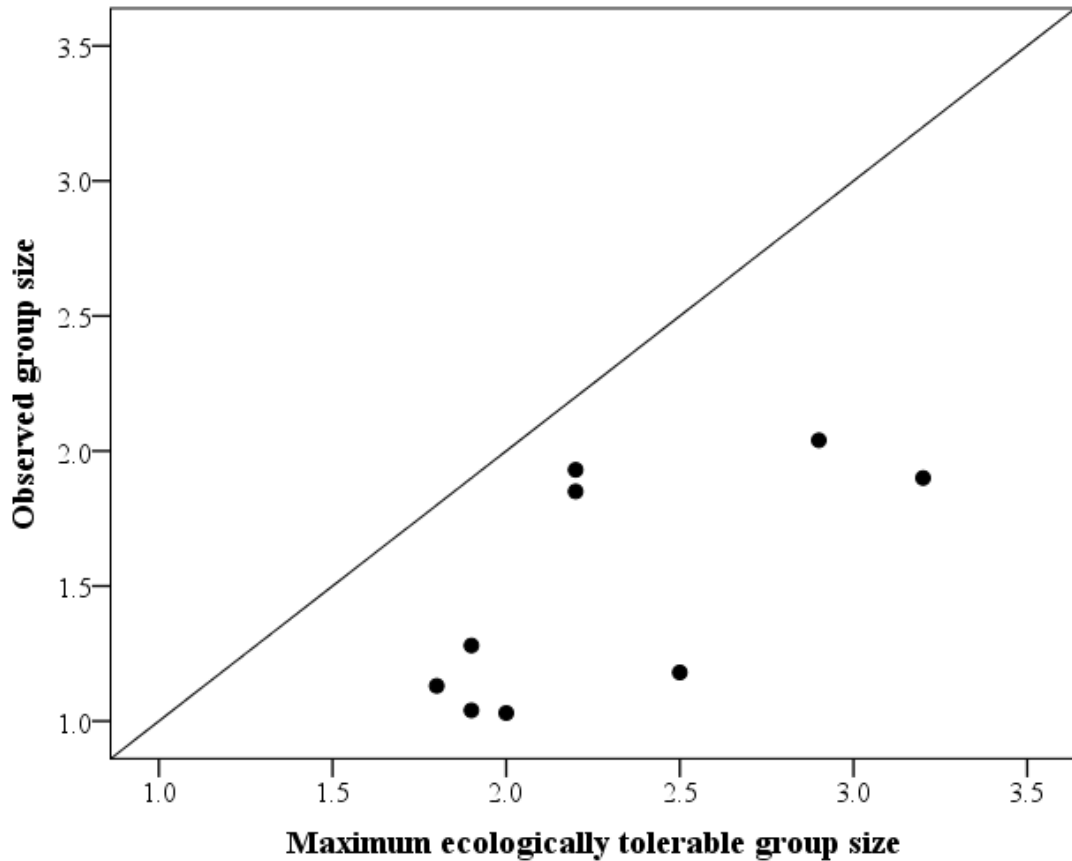


Figure 2.11: Observed group sizes versus predicted maximum ecologically tolerable group sizes (the line of equality is the line on which the maximum ecologically tolerable group size equals the observed group size).

Sensitivity analyses were performed to determine the robustness of the model to errors in parameter estimates. Parameters were both increased and decreased by 5% and 50% in turn. As there were 18 parameters, there were 36 model runs for changes of 5% and 36 model runs for changes of 50%. Measured across the grid, changes of 5% resulted in presence/absence distributions that were significantly different from the original model in only 1 of 36 runs, while changes of 50% led to significantly different distributions in 21 of 36 runs (all $\chi^2 > 3.84$, $df = 1$, $N = 374$, $P < 0.05$). Thus, the model was robust to small errors and sensitive to large errors in parameter estimates. Changing all parameters at once by both $\pm 5\%$ and $\pm 50\%$ led to significantly different presence/absence distributions than the original model in all four runs (all $\chi^2 > 11$, $df =$

1, $N = 374$, $P < 0.001$). This indicates that it is the particular set of parameter values obtained that is important.

These results were tested further by calculating the percentage agreement between the sensitivity analysis output and the original model predictions (Table 2.8). It is clear that changes of 5% led to model outputs that remain very similar to the predictions of the original model, for example 26 out of 36 runs had a percentage agreement of over 99% with the original model output. In contrast, changes of 50% lead to raster images that differ considerably more than changes of 5%, for example, only 8 of 36 runs had a percentage agreement greater than 99%. In addition, changing all parameter estimates at once led to a lower percentage agreement in all cases.

Table 2.8: Percentage agreement between the sensitivity analysis outputs and the original model predictions, where P_w is the precipitation of the wettest month, P_{wa} is the precipitation of the warmest quarter, T_s is temperature seasonality and T_{we} is the mean temperature of the wettest quarter.

Equation	Variable	+ 5%	- 5%	+ 50%	- 50%
Feeding	Intercept	99.71	99.72	96.72	96.13
Feeding	P_w	99.81	99.81	98.43	98.21
Feeding	Forest	99.32	99.36	90.55	91.74
Feeding	Leaves	99.82	99.84	96.14	98.92
Fruit	Intercept	98.04	98.39	79.81	91.59
Fruit	P_{wa}	95.25	96.30	80.13	91.57
Fruit	P_{wa}^2	96.69	96.86	80.13	91.57
Fruit	Forest	99.79	99.80	97.62	98.10
Moving	Intercept	99.02	99.46	75.16	99.16
Moving	T_s	99.01	99.42	73.29	99.16
Moving	T_s^2	99.66	99.72	93.36	99.16
Moving	T_{we}	99.62	99.72	91.23	99.16
Resting	Intercept	97.56	97.61	73.56	87.17
Resting	T_s	99.21	99.26	90.11	90.97
Resting	Forest	98.87	98.97	81.33	91.07
Resting	Party	99.50	99.52	94.67	93.92
Social	Intercept	99.98	99.98	99.82	99.82
Social	Party	99.996	99.996	99.96	99.96
All	All	73.82	90.11	73.01	87.17

2.3.3 Constraints on biogeography

Comparing the mean values for each time budget variable over all map pixels where orangutans were correctly predicted to be present (i.e. correct presences) with those where they were correctly predicted to be absent (i.e. correct absences) provides insights into the factors that may restrict orangutan biogeography. Average values for feeding time and the percentage of fruit in the diet were higher in correct presences than absences, while resting time was considerably higher in correct absences than correct presences (Table 2.9). Standard deviations were much higher in correct absences for

feeding time, resting time and the percentage of fruit in the diet, indicating a much wider range of predicted values than in correct presences.

Table 2.9: Mean and standard deviations for each time budget and diet variable in correct absences and correct presences (calculated using all pixels in these regions at a group size of one).

Variable	Correct absence		Correct presence	
	Mean	Standard deviation	Mean	Standard deviation
Feeding	21.72	17.20	26.21	7.66
Resting	58.31	29.77	26.51	12.76
Moving	12.10	4.66	12.45	4.19
Fruit	51.49	21.82	53.27	8.42

In order to statistically compare values for each time budget variable, they were compared between the grid locations where orangutans were correctly predicted to be present (correct presences, $n = 24$) with those where they were correctly predicted to be absent (correct absences, $n = 264$), producing similar results to those described above (Figure 2.12). Resting time was significantly higher in correct absences than in correct presences and feeding time and the percentage of fruit in the diet were significantly higher in correct presences than correct absences (Mann-Whitney U test_{resting}: $z = -5.770$, $N = 288$, $P < 0.001$; MWU_{feeding}: $z = -3.830$, $N = 288$, $P < 0.001$; MWU_{fruit}: $z = -2.357$, $N = 288$, $P < 0.05$). Moving time did not differ significantly between correct presences and correct absences (MWU_{moving}: $z = -0.594$, $N = 288$, $P = 0.552$).

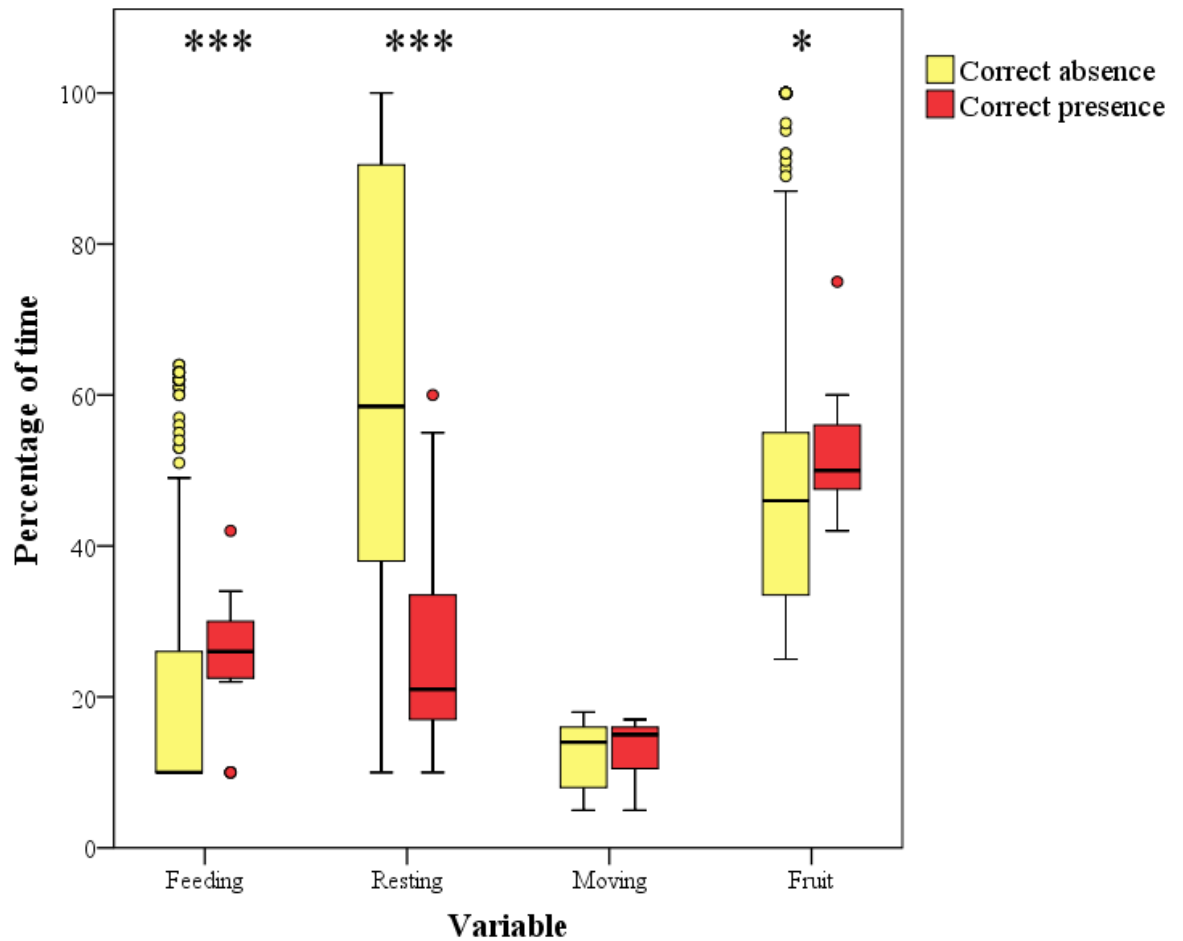


Figure 2.12: Boxplots of the predicted percentage of time spent feeding, resting and moving and the percentage of fruit in the diet at a group size of one at sites where orangutans were correctly predicted to be absent and correctly predicted to be present (for all boxplots, whiskers represent highest and lowest values and the box represents the upper quartile, median and lower quartile. Dots are outliers, * indicates that $P < 0.05$ and *** indicates that $P < 0.001$)

Predicted values were also compared between sites where orangutans were falsely predicted to live (false presences, $N = 71$) with locations where they were correctly predicted to live (correct presences, $N = 24$), to attempt to explain why orangutans do not live in these locations, even though the model predicts that they are suitable (Table 2.10). Average values were higher in false presences than correct presences for resting time, and for the percentage of fruit in the diet, and marginally so for feeding time. In contrast, average moving time was lower in false presences than correct presences.

Table 2.10: Mean and standard deviations for each time budget and diet variable at a party size of one in false presences and correct presences (calculated using all pixels in these regions at a group size of one).

Variable	False presence		Correct presence	
	Mean	Standard deviation	Mean	Standard deviation
Feeding	27.17	12.25	26.21	7.66
Resting	36.17	15.81	26.51	12.76
Moving	9.54	4.66	12.45	4.19
Fruit	56.62	13.55	53.27	8.42

Analysed across the grid, resting time was significantly higher in false presences than correct presences (MWU: $z = -3.779$, $N = 95$, $P < 0.001$; Figure 2.13). Moving time was significantly lower in false presences than correct presences (MWU: $z = -3.881$, $N = 95$, $P < 0.001$), while feeding time and the percentage of fruit in the diet did not differ significantly (MWU_{feeding}: $z = -0.356$, $N = 95$, $P = 0.722$; MWU_{fruit}: $z = -1.459$, $N = 95$, $P = 0.145$).

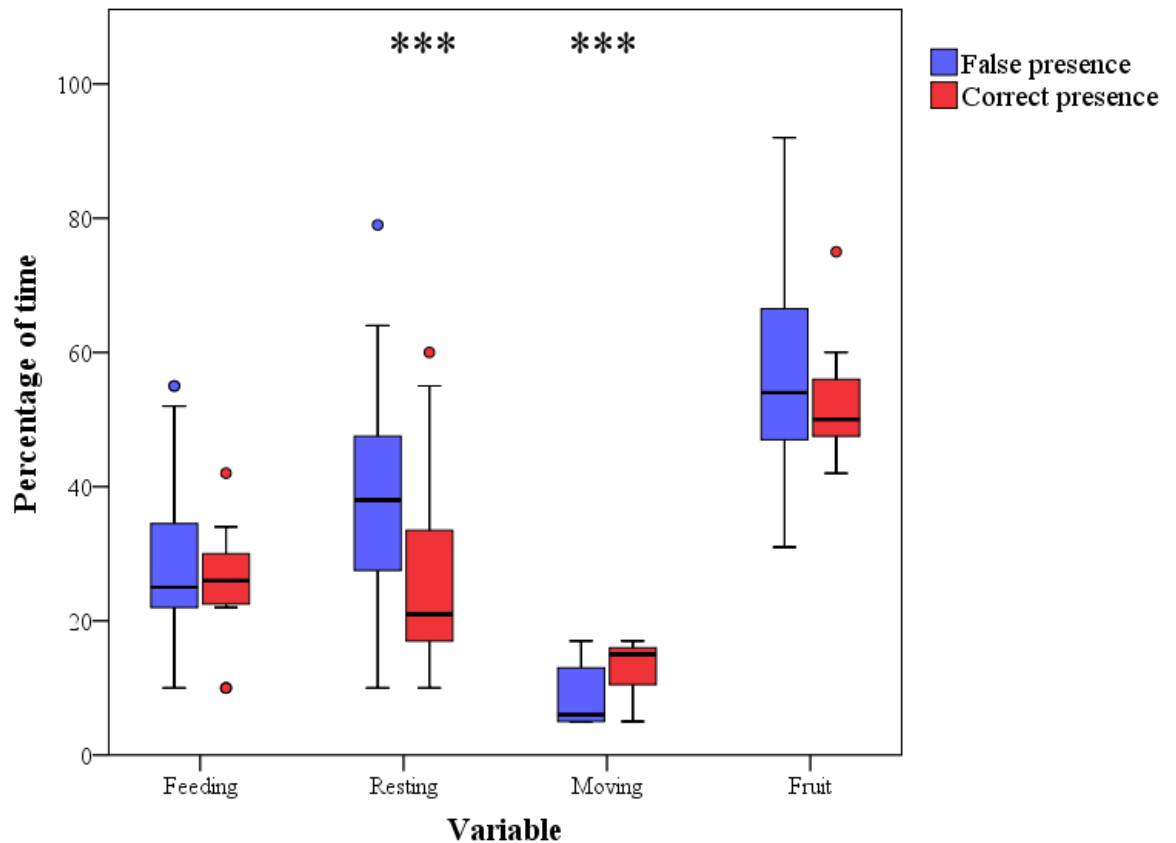


Figure 2.13: Boxplots of the predicted percentage of time spent feeding, resting and moving and the percentage of fruit in the diet at a group size of one at sites where orangutans were falsely predicted to be present and correctly predicted to be present (***) indicates that $P < 0.001$).

Finally, maximum ecologically tolerable group sizes were compared between false presences and correct presences, and found to be higher in correct presences than in false presences both on average (False presence mean = $1.89 \pm \text{SD } 0.55$; Correct presence mean = $2.16 \pm \text{SD } 0.39$) and when analysed across the grid (MWU: $z = -3.740$, $N = 95$, $P < 0.001$; Figure 2.14).

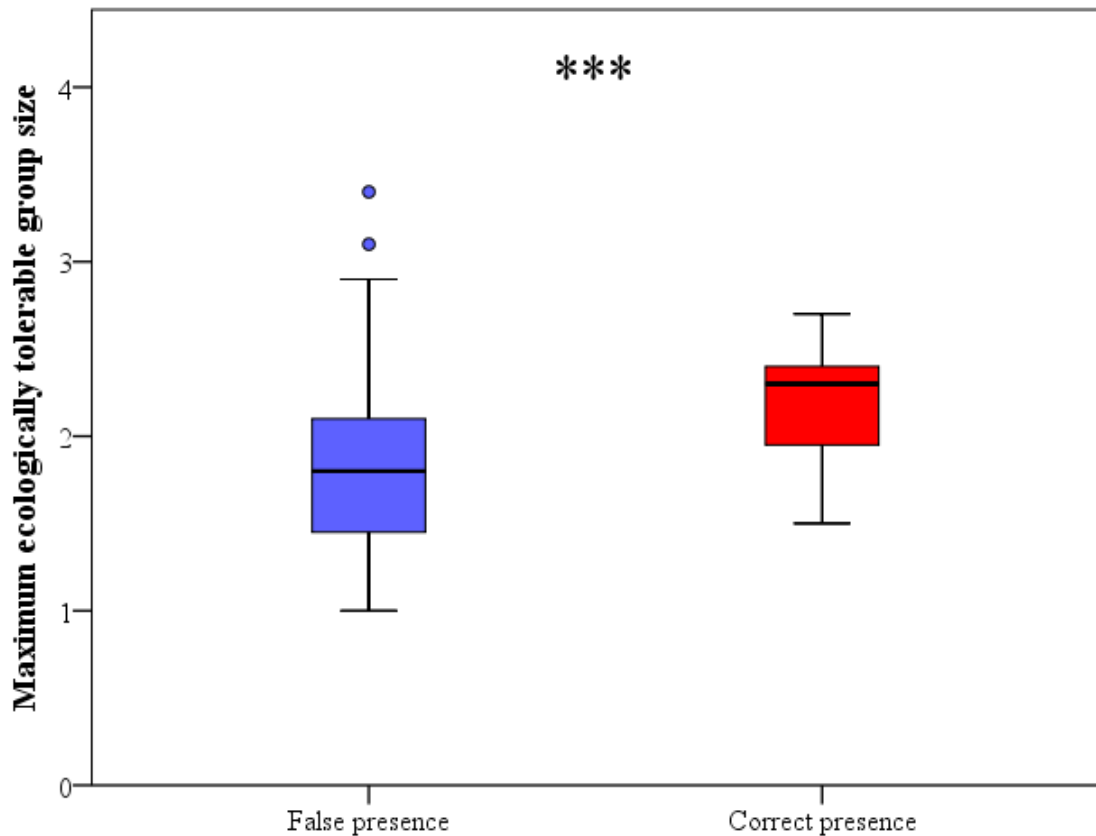


Figure 2.14: Boxplot of the maximum ecologically tolerable group sizes at sites where orangutans were falsely predicted to be present and correctly predicted to be present (***) indicates that $P < 0.001$).

2.3.4 Social organisation

Group size was found to be a major predictor of resting time allocations, with resting time demands increasing as group size increased (Table 2.5). The maximum ecologically tolerable group sizes that could be adopted were found to be very low across the range of the orangutan (Figure 2.15 and Figure 2.16), indicating low social flexibility. Average maximum ecologically tolerable group size was slightly higher in Sumatra than in Borneo (Sumatra mean = $2.25 \pm \text{SD } 0.50$; Borneo mean = 2.16 ± 0.38).

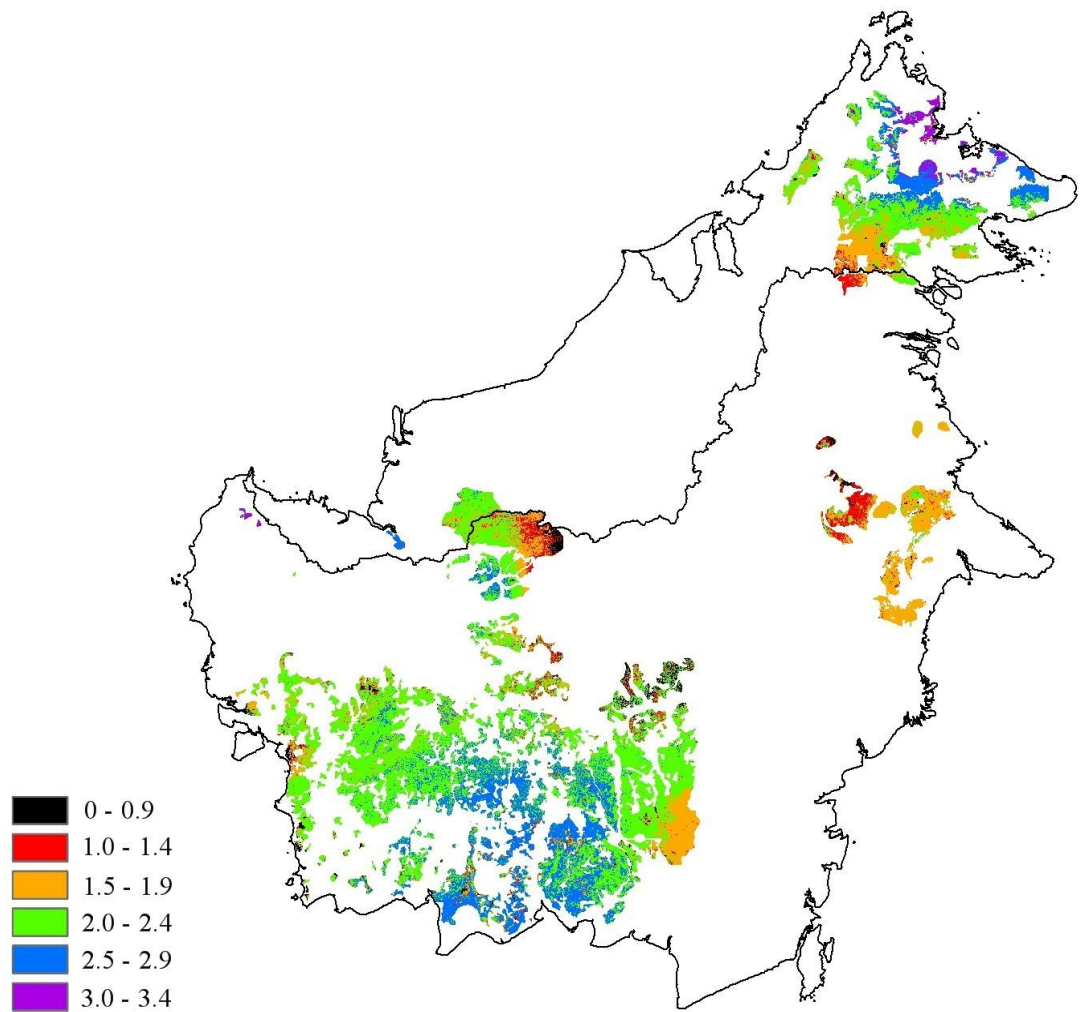


Figure 2.15: Predicted maximum ecologically tolerable group size within the current range of the orangutan in Borneo (lines indicate country boundaries).

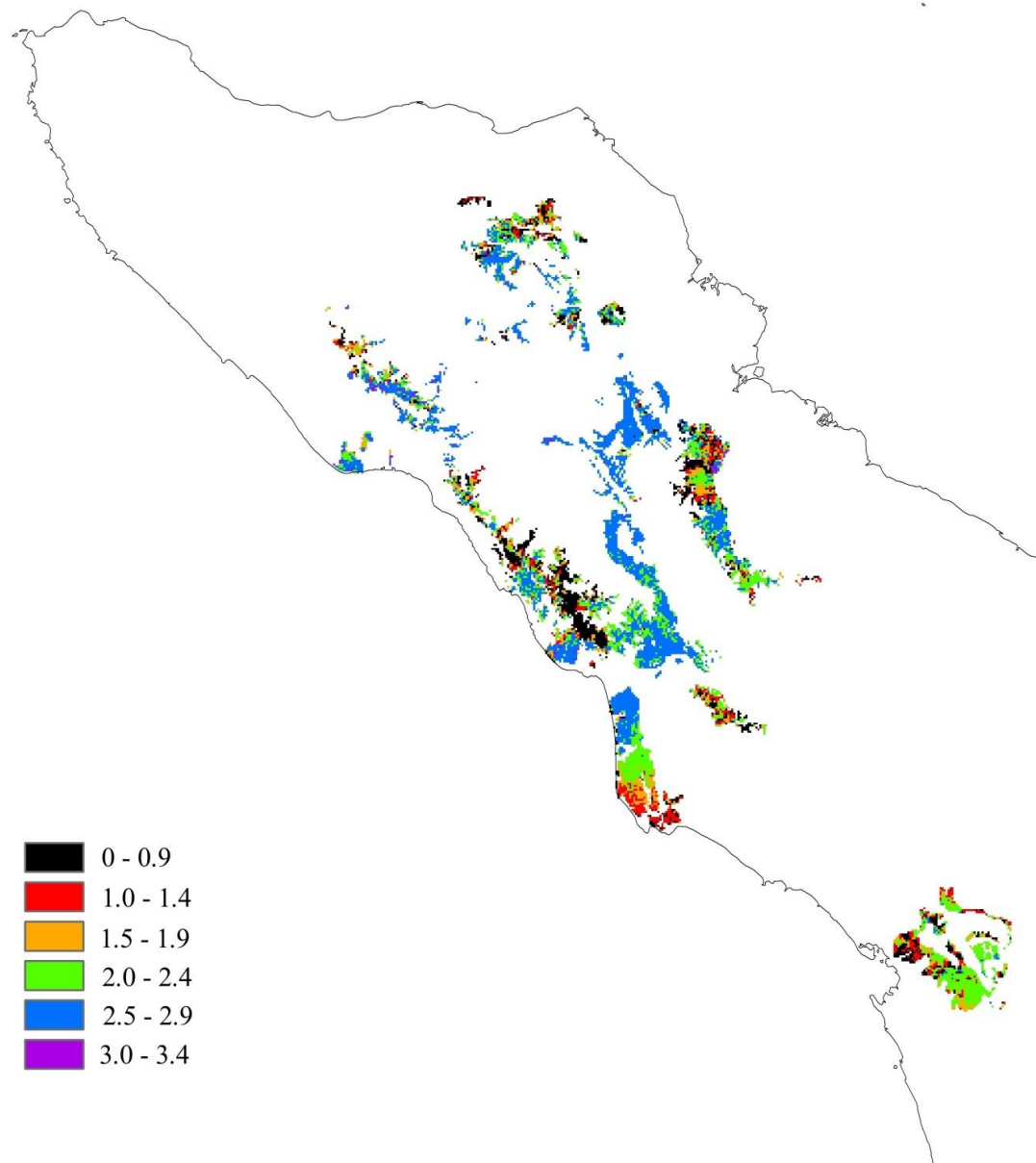


Figure 2.16: Predicted maximum ecologically tolerable group size within the current range of the orangutan in Sumatra.

2.4 Discussion

Time budget models have previously been shown to produce species distribution maps comparable in accuracy to bioclimate envelope models (Korstjens and Dunbar 2007, Willems and Hill 2009). Time budget models, however, have the additional advantage in that they can also be used to examine the factors that lead to particular distribution patterns and social systems. The time budget model created here produced an accurate map of the orangutan distribution and indicated that resting time is the key constraint that restricts the range of the orangutan and prevents them from living in larger groups. The results also suggest that the orangutan has limited social flexibility across its entire range and so is extremely vulnerable to habitat degradation.

2.4.1 Model Performance

The model correctly predicted the presence or absence of orangutans in 77.0% of map pixels, a similar level of accuracy to that obtained in previous time budget models. The majority of previous time budget models assessed the percentage of correct predictions based on a selection of discrete sites rather than all map pixels. These studies achieved accuracy rates of 84.3% for a model of the gorilla (Lehmann et al. 2008a), 74 % for the chimpanzee and 62% for the gorilla in a model that incorporated all African apes (Lehmann et al. 2008b), 85% for the baboon (Bettridge et al. 2010), 86% for black-and-white colobus monkeys and 84% for red colobus monkeys (Korstjens and Dunbar 2007). Finally, Willems & Hill (2009), in a model of the vervet monkey, assessed accuracy based on map pixels and achieved correct predictions in 87.4% of cells. Thus, the species distribution map produced in the current study is comparable in accuracy to previous time budget models.

Despite predicting the overall distribution of the orangutan encouragingly accurately, the model tended to overestimate orangutan ranges in certain areas, i.e. the model identified habitats as climatically suitable for the orangutan where they are not currently recorded to live. A number of possible reasons may help to explain these deviations. Firstly, areas may indeed be suitable, but dispersal barriers have prevented the orangutan from colonising them. In south-eastern Borneo, for example, the Barito and Mahakam rivers may have prevented the orangutan from ever entering this region, as orangutans are unlikely to attempt to cross wide rivers with fast flowing water (Rijksen and Meijaard 1999). Indeed, substantial populations of orangutans have never been found in this area of Borneo (Husson et al. 2009). Secondly, past and present hunting may have led to the extirpation of orangutans from climatically suitable regions. Although human population density was included to account for some of the effects of hunting, it is often performed by small groups of indigenous people that are unlikely to be characterised by high population densities. Archaeological evidence indicates that orangutans have been hunted for thousands of years by the indigenous people of both Borneo and Sumatra (Rijksen and Meijaard 1999, Harrison 2000). It has been suggested that the absence of the orangutan from areas in northern Borneo is the result of past hunting by indigenous people (Rijksen and Meijaard 1999) while the areas where sizable populations remain in Borneo are those inhabited by Muslim groups, who for religious reasons do not hunt the orangutan (Sugardjito 1995). Thus, many of the false presence locations, particularly those in northern Borneo, may be climatically suitable areas for the orangutans but represent locations where they have been extirpated by prehistoric human populations. Hunting by contemporary populations may also explain the absence of orangutans from otherwise suitable areas. Marshall et al. (2006) found that the distance to the nearest village known to hunt orangutans was the most important

predictor of orangutan density in East Kalimantan. Orangutans have an extremely slow reproductive rate (Knott et al. 2009, Wich et al. 2009) and therefore even relatively mild hunting pressures can have dramatic effects on orangutan population sizes (Singleton et al. 2004, Marshall et al. 2009). Thus, both past and current hunting by small-scale societies can significantly impact on the distribution of the orangutan, and may explain why orangutans are not found to live in some of the areas in which they are predicted to be able to survive.

Many of the locations in which the orangutan is absent but the model predicted them to live were those adjacent to its current range. The range of the orangutan has contracted dramatically in the past century, and has become increasingly fragmented (Husson et al. 2009). The estimated distribution of the orangutan in 1930 indicates that it once ranged much more continuously across southern Borneo and along the eastern coast (Rijksen and Meijaard 1999). In Borneo, 45.2% of the areas in which the orangutan was predicted to live, but has not recently been observed, are within the orangutan's 1930 range. These areas may therefore be climatically suitable, but uninhabited by orangutans as a result of recent anthropogenic effects.

Another issue that causes inaccuracies in any kind of climate model is the limited availability of accurate and recent data on species distribution patterns, land cover and climate. Although a very recent land cover map was used in the current study, orangutan distribution patterns were based on data from 2007, and so recent orangutan distribution shifts in response to land cover change are not reflected in the distribution data. In fact, applying the 2010 land cover map to the observed range of the orangutan in 2007 showed that a large proportion of this range is now categorised as plantations and regrowth. This highlights the extremely rapid rate of deforestation and habitat

fragmentation which threaten the orangutan with imminent extinction. It also suggests that the habitat distribution map from 2007 may now be overestimating the remaining range of the orangutan, and that the actual situation may be considerably worse, particularly if extinction debt is taken into account (Tilman et al. 1994). There is evidence that a large number of primate populations are already doomed to extinction following the fragmentation of their habitats, but that this is a time-delayed process, and therefore represents an extinction debt that has yet to be paid (Tilman et al. 1994, Cowlishaw 1999). Therefore a number of the populations recorded in the 2007 census may already have disappeared or be moving inexorably towards extinction and therefore cannot be considered viable populations.

The climate data used here were also limited, being based on long-term averages over a period of 50 years. This means that the effect of recent land conversion on both regional climates and microclimates is not well represented in the data. Deforestation and subsequent changes in land use can have strong impacts on local climates (Bonan 2008); for example, oil palm plantations have been shown to have a hotter and drier microclimate than forests during the day (Luskin and Potts 2011). Large scale land-use changes can affect climates over wider areas; a model of deforestation in the Amazon suggested that this could lead to a global reduction in precipitation (Werth and Avissar 2002). Local and global climatic changes not represented in the data may mean that areas that were previously suitable habitat are now unsuitable, particularly areas at the edge of forests where these changes may be more pronounced (Fischer and Lindenmayer 2007). This may therefore account for some of the false presences in the model.

Finally, the model predicted orangutans to be absent from a number of locations where they were recorded to be present in 2007. Most of these locations were adjacent to those

known to contain orangutans. The distribution of orangutans is often extremely patchy, with densities varying spatially and temporally in accordance with food availability (McConkey 2005). Thus, there are likely to be areas that do not clearly fit into a strict definition of presence or absence, for example, those used by roaming males (Husson et al. 2009). This may explain why orangutans have been observed in areas in which the model did not predict them to be able to exist. This is supported by the fact that 58.3% of these false absences were in pixels categorised as plantations or regrowth in the land cover map, and are therefore unlikely to support breeding populations, but may be used irregularly by orangutans with ranges on the borders of the forests. In addition, these areas may represent locations that have been converted to plantations since the orangutan distribution data were collected; indeed 75.2% of these plantations were categorised as forest in 2000. Forest cover in South-east Asia declines by around 1% per year (Miettinen et al. 2011a), and much of the 2007 range may therefore now be unsuitable for the orangutan.

There is, however, some evidence that orangutans can persist in acacia plantations, although the long-term viability of these populations is not known (Meijaard et al. 2010a). It is therefore possible that excluding all plantations/regrowth as unsuitable is an overly pessimistic outlook, and that the orangutan can in fact survive in some of these locations, particularly those adjacent to old growth forest.

2.4.2 Constraints on biogeography

One of the major advantages of time budget models is that they can be used to investigate the factors that act to constrain distribution patterns. Among orangutans, resting time appears to be the key constraint on biogeography, as resting time allocations were much higher in areas in which the orangutan was correctly predicted to

be absent than areas in which it was correctly predicted to be present. This relationship was found to be significant when analysed across the grid of 374 points separated by 0.5° longitude and latitude and seems to be linked to diet, forest cover and temperature seasonality. Measured across the grid, the percentage of fruit in the diet was significantly higher within the locations where the orangutan was correctly predicted to live, than in those locations that were correctly identified as unsuitable. This indicates that fruit availability may act to constrain distribution patterns, as in regions with little fruit orangutans would have to eat more fallback foods, which require increased digestion time. Forest cover was also a significant predictor of resting time, in addition to the percentage of fruit in the diet. In sparsely forested areas the model therefore predicts a low percentage of fruit in the diet and high resting time requirements, while in heavily forested areas the model predicts a high percentage of fruit in the diet and low resting time.

The model results therefore suggest that large areas of Borneo and Sumatra are unsuitable for the orangutan due to a lack of forest cover and fruit availability. Although Hardus et al. (2012) found that orangutans spent more time feeding on fruit in logged areas, the majority of findings suggest that more degraded forests have lower fruit availability and are therefore less suitable habitat. In logged areas it was shown that there are fewer large food trees (Felton et al. 2003) and orangutans eat a higher proportion of leaves than in primary forest (van Schaik and Rao 1997). Similarly, in the heavily degraded habitat of Batang Serangan, orangutans were found to rely heavily on bark (Campbell-Smith et al. 2011b), while orangutans found living in acacia plantations also seem to obtain a large proportion of their energy from cambium (Meijaard et al. 2010a). Thus, it seems likely that areas with reduced forest cover will provide less fruit resources for orangutans, which may prevent their habitation. Interestingly, in correct

presences all values for fruit are relatively clustered around the mean. This indicates that the orangutan diet may not be very flexible, and that it may struggle to survive on a diet of less than about 40% fruit.

Resting time was predicted to be restrictively high in areas with low forest cover and low fruit consumption. Low forest cover may increase exposure to the sun, forcing orangutans to spend more time resting to prevent overheating (Pollard and Blumstein 2008). During periods of low fruit availability, orangutans increase their time spent resting and spend less time moving and feeding (Knott 1998). It has been suggested that this strategy may also be used in degraded habitats where food availability is lower (Johnson et al. 2005). Gorilla distributions have also been shown to be primarily constrained by resting time, which was interpreted as a result of an increased reliance on fallback foods in more marginal habitats (Lehmann et al. 2008a). It is interesting, however, that the only two studies to have investigated orangutan behavioural changes in response to logging found that resting time was actually lower in logged forests (van Schaik and Rao 1997, Hardus et al. 2012). These studies compared values within individuals that spent time in both logged and unlogged forest. It is therefore possible that these individuals move quickly through the logged forest (indeed moving time was elevated in both studies) in order to reduce the time spent in these less preferred regions. These results can therefore not be viewed as indicative of the expected time budget allocations for orangutans living permanently in a logged region. The study by van Schaik and Rao (1997) did show that orangutans ate a greater proportion of fallback foods while in the logged forests, due to a reduced availability of fruit in these regions. It can therefore be assumed that if the orangutans did remain permanently in these areas, they would be forced to spend considerable time resting to digest these lower quality foods.

Resting time was also significantly higher in areas that orangutans were predicted to inhabit, but are not currently recorded to live, than in locations that were correctly predicted to be unsuitable. This implies that there is a maximum amount of time that orangutans can realistically devote to resting, above which they can not survive. Korstjens et al. (2010) investigated resting time across 78 African and American primate species and found that they would struggle to survive in locations that required more than 33% enforced resting time. Many of the resting time estimates in the areas where the orangutan was predicted to live, but is not currently known to occur, fall above this threshold. It therefore seems probable that orangutans are prevented from living in many of these locations as a result of high resting time demands. Thus, orangutans, like other primates, appear to be restricted by a maximum value of resting time, and this may be what is preventing them from living in some of the areas that were predicted to be suitable by the model.

It is important to mention in relation to resting time that the model used here predicts total resting time rather than enforced resting time, a measure that has been used in a number of previous models as a more accurate representation of necessary resting time (Lehmann et al. 2008b, Bettridge et al. 2010, Korstjens et al. 2010). This is because there are two components of resting time; enforced resting time (that required for the digestion of food or for thermoregulation) and uncommitted resting time (a reserve of free time that can be allocated to other essential activities). It is important to include only enforced resting time in a time budget model, as this is the time that an animal needs to devote to resting in order to survive. A generic equation for enforced resting time in primates has been generated (Korstjens et al. 2010), but this produced extremely low values of enforced resting time for orangutans. Therefore, a regression equation was obtained from the observed data. As this equation has a high explanatory power this

indicates that very little resting time is in fact uncommitted (Lehmann et al. 2008a); therefore it can be assumed that the equation is predicting values very close to that required for enforced resting time. However, it is probable that the resting time estimates produced by this model are slightly higher than those required in reality.

In contrast to the resting time results, moving time was significantly higher in locations that were correctly predicted to be suitable than locations that were predicted to be suitable, but where the orangutan is not known to occur. This can be interpreted as a strong indication that moving time is not a restrictive factor preventing the orangutan from inhabiting these ‘false presence’ locations.

Feeding time was found to be significantly higher in locations in which the orangutan was correctly predicted to survive than in locations correctly predicted as unsuitable. This implies that the locations that are unsuitable for habitation overall provide the ‘best’ environments in terms of feeding time, which seems rather counterintuitive. This is likely to be the result of the positive relationship between feeding time and forest cover; as forest cover increases, feeding time also increases (possibly a result of the availability of higher quality foods that require greater extraction times). Comparing the map of feeding time across Borneo and Sumatra with that of forest cover, it becomes clear that many of the locations with very low predicted feeding time values are in southern Sumatra, where intense deforestation has reduced forest cover to extremely low levels. This leads to very low predicted values for feeding time, which are not likely to be representative of reality. It seems probable that this is a result of using linear regression. The linear relationship between feeding and forest cover is based on a sample size of only 11, with forest cover ranging from 33 to 80%. The linear equation produced can not, however, tell us anything about the relationship between feeding and forest cover at levels of forest cover lower than 33%, which is most likely not a

continuation of this linear relationship. Therefore, calculating a value for feeding time at forest cover values of 0-10%, as in much of southern Sumatra, is extrapolating beyond the data, and therefore may give unrealistic values. However, in terms of the overall model, this is not a problem as these locations are deemed as unsuitable both by the other time budget components and also the land cover data.

Finally, maximum ecologically tolerable group sizes were compared, and were found to be higher in locations that were correctly predicted to be suitable than the locations that were predicted to be suitable but where orangutans are not known to occur. This indicates that taking a minimum group size of one may be unrealistically low and that the orangutan may not be able to live in complete solitude; indeed, for orangutans to survive in the long-term, they must average group sizes of greater than one in order to reproduce. This may help to explain why the model overestimated the range of the orangutan in some areas.

2.4.3 Social organisation

Group size was found to be a major predictor of resting time allocations, with resting time demands increasing as group size increased. This is in concordance with evidence that at Tanjung Puting in Borneo, resting time was found to increase on days when orangutans formed social groups (Galdikas 1988). This indicates that sociality in orangutans may have high costs in terms of resting time, which could help to explain their largely solitary social system. This can probably be attributed to the effect of food competition, which has been suggested as the major constraint on orangutan sociality (Sugardjito et al. 1987, van Schaik 1999). Fruiting trees in South-east Asian rainforests are mostly small and dispersed, and so a single orangutan can usually consume all of the fruit from a tree in one feeding bout (Knott and Kahlenberg 2007). In larger groups

there is more competition for food and fruit trees will be depleted more rapidly. As a result, orangutans may be forced to eat more fallback foods such as leaves and bark, which require longer digestion times and therefore force the animals to devote more time to resting (Galdikas 1988). Similarly, group size in black-and-white colobus monkeys was found to be restricted by resting time due to a diet heavily based around folivory. These high resting time demands limit time available for social behaviour, which then limits group size (Korstjens et al. 2006). It has also been shown that for primates more generally, resting time is a key constraint that has influenced the evolution of group size. Over 50 primate species, a negative relationship was found between group size and resting time, suggesting that resting time has been an important constraint on the evolution of group size in primates (Pollard and Blumstein 2008). Resting time is therefore an important constraint on primate grouping patterns and appears to be a major contributing factor to the relatively asocial nature of the orangutan.

The results indicate that the orangutans do not tend to live in group sizes that equal or exceed the maximum ecologically tolerable group size. This is in contrast to other time budget modelling studies that found that at between 8 and 44% of sites, observed mean group size exceeded the predicted maximum ecologically tolerable group size (Dunbar 1992a, Dunbar 1992b, Lehmann et al. 2008a, Lehmann et al. 2008b, Willems and Hill 2009, Bettridge et al. 2010). This difference is likely to be related to the intensity of both predation risk and ecological constraints. Orangutans experience relatively low levels of predation risk, as their only predators are clouded leopards and, in Sumatra, tigers (van Schaik 1999). The benefits of grouping are therefore likely to be less than in species that suffer heavily from predation pressure, where high levels of predation may force them occasionally to live above the maximum sustainable group size. It may

therefore be advantageous for the orangutan to live in group sizes lower than the maximum, especially as the relatively unproductive environment means that ecological constraints are high. Similarly, observed mean group sizes in gorillas, which also suffer less from predation pressure, were smaller than the maximum ecologically tolerable group size at 12 out of 13 sites (Lehmann et al. 2008a). Thus, adopting group sizes lower than the maximum possible may be an advantageous strategy that allows orangutans to obtain some of the other benefits of sociality such as protection from harassment and socialisation of infants (van Schaik 1999), while incurring less of the costs associated with grouping, such as high resting time requirements.

However, all of the predicted maximum ecologically tolerable group sizes across Borneo and Sumatra were relatively low, with values of around 2 predicted for most of the orangutan's current range. This implies that orangutans generally do not have a large range of group sizes available to them; therefore overall social flexibility is relatively limited. This is interesting in comparison to the other species of great apes that all live in larger and more cohesive groups. Although chimpanzees have a fission-fusion social system, their average party size far exceeds that of the orangutan (Chapman et al. 1994, Boesch 1996, Newton-Fisher 1999, Lehmann et al. 2008b). This study indicates that the alternative and more solitary social system adopted by the orangutan is a response to the intense feeding competition that occurs in aggregations, imposing high resting time demands. This finding is in accordance with the current consensus on orangutan sociality, which attributes their asocial nature to the high ecological costs of grouping caused by the low productivity of South-east Asian forests, which creates high feeding competition (Sugardjito et al. 1987, van Schaik 1999). Indeed, predicted maximum ecologically tolerable group sizes across Borneo and Sumatra appear to correspond strongly to the observed productivity of the forests. Regions in the East of Borneo were

characterised by particularly low maximum ecologically tolerable group sizes. These areas, as well as those in the North-east of Borneo, are inhabited by the subspecies *P.p. morio* and it has been suggested that these forests are the least productive in which the orangutan is found (van Schaik et al. 2009a). Fruit productivity has been shown to be higher on Sumatra than Borneo (Wich et al. 2011) and on average the model did predict slightly larger maximum ecologically tolerable group sizes for Sumatra. The time budget model clearly supports the hypothesis that the productivity of the rainforest has a strong influence on constraining grouping patterns in this species. Orangutans are thought to have been more social in the past, but the climatic changes that occurred during the late Miocene-Pliocene caused the tropical rainforests to become less predictable, forcing the orangutans into a more dispersed social system (Harrison and Chivers 2007). Indeed, in captive conditions, where ecological constraints are minimal, higher levels of social behaviour have been observed (Edwards and Snowdon 1980, Zucker and Thibaut 1995, Salina et al. 2004, Claßen 2011). The results presented in this chapter provide further support for this argument but also identify the possible mechanism by which ecological constraints restrict group size; it is the high resting time demands which may be caused by an increased reliance on fallback foods that appear to prevent higher levels of sociality.

2.4.4 Insights for orangutan conservation: social flexibility as an indicator of vulnerability

The distribution of maximum ecologically tolerable group sizes can provide insights into the level of time budgeting stress faced by different populations. It is clear that the populations in eastern Borneo, as well as a few patches in northern and central Borneo, are under considerable time budgeting stress, as their maximum ecologically tolerable

group sizes are close to one. The populations in these areas are being forced to live close to the minimum group size, which means that they are living at the limit of their social flexibility in order to fit all of their time budgeting demands into the time available in a day. Any changes to their habitat, such as deforestation, an increase in the intensity of human exploitation of, or encroachment into the forest could lead to increases in time budget allocations, for example by reducing the availability of food leading to increases in feeding, moving or resting time. Populations already at the limits of their flexibility cannot respond to these changes by reducing group sizes, thereby freeing up time for these essential activities. Orangutans living under these conditions would therefore be unable to fulfil the behaviours necessary for survival. These populations are therefore particularly vulnerable to further habitat degradation, which could rapidly drive them to extinction. Maximum group sizes predicted by the model are relatively low across the entire range of the orangutan, which indicates that even in prime habitat, orangutans do not have a great deal of flexibility available to them. This suggests that even in the best habitats, orangutans are unlikely to be able to withstand extensive environmental damage.

Given the evident vulnerability of the orangutan, it is concerning that the anthropogenic variables that were incorporated into the model had such a strong impact on the accuracy of the predictions. The addition of the land cover and human population density data improved model predictions from 44.5% accuracy to 77.0%. Given that the original model already included forest cover as an important explanatory variable, this clearly highlights the extreme importance of anthropogenic factors in determining the distribution of the orangutan. This provides additional support to the argument that human impacts such as hunting and deforestation have been a major determinant of the recent decline of the orangutan (Delgado and van Schaik 2000, Goossens et al. 2006).

2.5 Conclusion

In this chapter, the distribution of the orangutan was explored using a time budget modelling approach with the additional use of land cover and human population density data. Results highlight the extremely vulnerable position of the two orangutan species. Evidence was presented that high resting time demands, related to diet and forest cover, prevent the orangutan from living in much of Borneo and Sumatra, including many regions that made up parts of its previous range. Maximum possible group sizes are relatively low, indicating that the orangutan has limited social flexibility. In many regions, predicted maximum ecologically tolerable group sizes are close to the minimum permissible value, indicating that in these areas, the orangutan is particularly vulnerable to extinction. Orangutans are clearly in a critical position, where even small changes to their habitat caused for example by further deforestation or future climate change, or demographic disturbances such as disease epidemics, may have drastic consequences.

3. The Effects of Climate Change and Human Population Growth on the Distribution and Behaviour of the Orangutan

3.1 Introduction

3.1.1 The threat of climate change and human population growth to the survival of the orangutan

Climate change represents a severe threat to biodiversity across the globe (Thomas et al. 2004). In many cases habitats will become unsuitable for survival and species will either be forced to shift their distributions in line with the climate or, where this is not possible, will become extinct (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2005). Increasing pressures from a growing human population will restrict the ability of species to adapt their ranges, while exacerbating human impacts on remaining habitat. Orangutans are already on the brink of extinction and so any additional pressures are likely to have devastating consequences. Deforestation has destroyed a huge proportion

of the available tropical rainforest in Borneo and Sumatra, and so the orangutan is not likely to be able to shift its distribution into regions that become newly suitable under future climates. It is therefore essential for the conservation of the orangutan that the effects that climate change and human population growth will have on the current distribution of the species are predicted, and the areas that may remain suitable under future climates identified. In order to protect this species in the future, it is vital that such predictions are incorporated into conservation initiatives, to ensure that the limited resources are distributed in the most effective manner.

In addition to shifts in distribution patterns, climate change may also force species to alter their behaviour in order to adapt to the changing environments. Climate change may, for example, lead to reductions in the availability of food, forcing animals to spend more time feeding or moving in order to meet their nutritional requirements. If competition for food increases, grouping may become more costly, forcing a species to form smaller groups. In order to gain an in-depth understanding of the range of effects that climate change may have on a species, it is therefore also important to predict the behavioural changes that may occur in the future.

The investigation of the potential effects of climate change on species' distributions is a major focus of conservation biology (Guisan and Thuiller 2005, Sinclair et al. 2010) and numerous predictive models have been developed. The majority of these models utilise correlations between the observed distribution of a species and climate variables to produce a 'climate envelope' in which the species is predicted to live (Pearson and Dawson 2003). However, these models provide little insight into the mechanisms that determine distributions or the effect that climate change will have on behaviour (Lehmann et al. 2010a), and rarely incorporate the important effects of human population growth. In contrast, time budget models have been developed that

incorporate behaviour as an intermediate link between climate and survival, allowing for a more in-depth analysis of the factors that limit distribution patterns. Human population growth can also be included in these models (Chapter 2). Time budget models can identify probable future distributions, and predict the potential effects of climate change on behaviour and sociality (see Dunbar et al. 2009 for a review), information that is invaluable for conservation.

3.1.2 Climate change

The origins of climate change science date back nearly 200 years, to 1824 when Jean Baptiste Fourier first described the natural greenhouse gas effect (Fankhauser 1995). It was not until the turn of the 20th century, however, that a Swedish scientist, Svante Arrhenius, recognised the potential for man-made emissions to affect the carbon cycle (van Dyke 2008). Since the 1950s the issue of climate change has become increasingly prominent in science, government, non-governmental organisations and the public sphere (Agrawala 1998). In 1988, the Intergovernmental Panel on Climate Change (IPCC) was founded by the World Meteorological Organisation and the United Nations Environment Programme to provide a clear review of the scientific evidence behind climate change (IPCC 2012). This organisation has compiled evidence from thousands of studies that demonstrate patterns of past climate change and provide clear predictions for the future of the climate system.

Over the past century the global climate has warmed by around 0.6°C (Walther et al. 2002). Warming has been more pronounced over land than the oceans, and night time warming has been more rapid than day time warming (Hulme 2005). In the coming century, the IPCC predicts that climate change will continue, with warmer temperatures, decreases in snow cover and sea ice, and an increased frequency of extreme heat waves

and heavy precipitation (Solomon 2007). Global temperatures are predicted to increase by between 1.1 and 6.4°C by 2090-2099, depending on the emissions scenario used to formulate the predictions (Solomon 2007). Overall precipitation is likely to increase at high latitudes, but is expected to decrease in subtropical regions (Solomon 2007). Over the past 700,000 years the climate has been oscillating from glacial to interglacial conditions; however, future warming in response to anthropogenic factors is likely to push the climate outside the range of these past conditions, to which all current ecosystems have adapted (Overpeck et al. 2005).

3.1.3 Climate change and species distribution models

Species distribution models have been developed as a tool to investigate the shifts that can be expected to occur under future climate scenarios. These models are now employed by a number of conservation NGOs, academic institutions and government agencies to assist in the design of conservation responses to future climate change (Hagerman et al. 2010). The majority of species distribution models use a correlative approach that is based on ecological niche theory, and are termed bioclimate envelope models (Pearson and Dawson 2003). Hutchinson (1957) first defined the fundamental niche of a species as the environmental conditions within which a species could survive. This contrasts with the realised niche, which is the part of the fundamental niche in which the species actually lives, once the added biotic constraints have been included (van Dyke 2008). Bioclimate envelope models, in contrast, deal with the ‘climate niche’, the part of the fundamental niche that is determined solely by climatic factors; therefore they do not incorporate any other environmental variables or biotic factors (Pearson and Dawson 2003). These models are designed to predict the climate niche of a species, i.e. the areas that are climatically suitable for their survival, the ‘climate

envelope'. In order to do this, the presence or absence of a species at known locations is correlated with climate variables. These correlations can then be used to project species distributions across the region, thereby highlighting all of the areas in which the climate is suitable for survival (Pearson 2006). If climate data can then be predicted for the future, these can be added into the models, and the future distribution of the species predicted.

Bioclimate envelope models have been heavily criticised on the grounds that they do not incorporate important biotic interactions. Factors such as competition, predation and symbiosis with other species have important effects on species distributions but are not included in the models (Hampe 2004, Harrison et al. 2006, Lawler et al. 2009). Models have also been criticised for extrapolating beyond known climates (Dormann 2007, Fitzpatrick and Hargrove 2009), and for excluding the effects of geographical barriers, soil and geological conditions (Duncan et al. 2009), habitat degradation, overexploitation, the effects of invasive species (Brook et al. 2009), evolutionary changes, phenotypic plasticity, genetic variability (Dormann 2007), and differences in dispersal abilities (Lawler et al. 2009). However, the inclusion of all of these additional factors would lead to extremely complex models which would require huge quantities of detailed data and computing power. Bioclimate envelope models on the other hand, provide a relatively simple method of determining a first estimate as to the effects of climate change on a species, information that can be extremely useful for conservation (Pearson and Dawson 2003). These models have been widely utilised to predict future distributions of, for example, plants (Berry et al. 2002, Miles et al. 2004, Pearson et al. 2004), butterflies (Beaumont et al. 2005), birds (Virkkala et al. 2008, Gasner et al. 2010), amphibians and reptiles (Araujo et al. 2006), koalas (*Phascolarctos cinereus*; Adams-Hosking et al. 2011), snakes (Penman et al. 2010), European mammals

(Levinsky et al. 2007) and mosquitoes (*Anopheles spp.*; Peterson 2009). As long as the limitations are recognised, it appears that bioclimate envelope models can provide valuable contributions to conservation biology (Pearson and Dawson 2003).

3.1.4 Climate change and time budget models

Time budget models are similar to bioclimate envelope models in that they use the same climate data to predict species distributions, and in fact produce very similar predictions (Willems and Hill 2009). However, time budget models include an additional level to the modelling process; behaviour. Using this approach provides a more detailed understanding of the factors that restrict distributions and allows future behavioural changes to be predicted (Lehmann et al. 2010a). Time budget models therefore provide additional information about the mechanisms by which climate influences distributions and about how the behaviour of the species will change.

Three previous studies have used time budget models to investigate the effect of climate change on species distribution patterns, all three of which focus on primates. Gelada were predicted to be forced into higher altitudes as the climate warms, considerably reducing their range and potentially isolating subpopulations living on different mountain peaks (Dunbar 1998). Lehmann et al. (2010) investigated the effect of climate change on gorillas and chimpanzees, both in terms of their future distribution as well as potential behavioural changes. It was predicted that even if gorillas responded with extreme behavioural flexibility, by adopting a fission-fusion social system, their range may still be dramatically reduced under future conditions. Chimpanzee distribution patterns were predicted to be less affected by climate change than their larger bodied relatives; however, their group sizes may be greatly reduced in the future. Chimpanzee survival may therefore be strongly dependent on the minimum viable group size that

they can adopt. In addition, both chimpanzees and gorillas were predicted to experience an increase in resting time in the future at the locations in which they survive, and this is likely to be a result of changes in diet and the increased temperature (Lehmann et al. 2010a). Korstjens et al. (2010) predicted that increases of 2°C or 4°C would greatly reduce the distribution of African folivores due to the impact on their enforced resting time. In contrast, the enforced resting time of New World folivores and non-folivores remained virtually unaffected by these climate change scenarios, indicating that enforced resting time will not be an important restricting factor for these species.

These studies demonstrate the types of predictions that can be obtained using time budget models. Despite their evident utility, these models have yet to be widely applied, even within the field of primatology.

3.1.5 Climate change and the orangutan

Current information on the effect that climate change is likely to have on the orangutan is extremely sparse. Gregory et al. (2012) used a boosted regression tree species distribution model to predict the effect of climate and land cover change on orangutans in Sabah. This model was based on relationships between orangutan nest count data and the climate, habitat variables (e.g. forest cover) and anthropogenic variables (e.g. distance to roads). The model incorporated a land cover change model which projected observed deforestation rates to 2100. Overall, land cover was found to have the greatest influence on orangutan population sizes. Under future climates, the distribution of the orangutan in this region was predicted to shift westwards as habitat suitability was predicted to decline in the eastern forests but improve in western Sabah (Gregory et al. 2012). This model clearly provides valuable insights into the future of orangutans in

Sabah, but there are no studies to date that predict the effect of climate change on the overall distribution of the orangutan across Borneo and Sumatra.

There is, however, evidence to suggest that climate change may have severe consequences for the forest habitat on which orangutans depend. In particular, plant phenology is likely to be affected (Schuur 2003). Rainfall has an important influence on the timing of production by tropical plants, and changing precipitation patterns may disrupt the mechanisms that control this timing (Wright 1996). An increase in rainfall may lead to a reduction in the net primary productivity of tropical forests (Schuur 2003). If climate change was to disrupt fruiting patterns or reduce fruit availability or quality in Borneo and Sumatra, this could have dramatic effects on the orangutan's ability to survive, as their diet depends heavily on large quantities of fruit (Russon et al. 2009). In addition, there is some evidence to suggest that an increase in atmospheric carbon dioxide will lead to a reduction in the nutritional quality of leaves (Coley 1998, Clark 2004), which is an important fallback food for orangutans in times of fruit scarcity (Wheatley 1982, Galdikas 1988, Knott 1998). Climate change may also lead to forest dieback which would prevent orangutans from living in particular regions (Bonan 2008). In the past, the South-east Asian rainforest has been fairly sensitive to climate change (Heaney 1991). However, in tropical regions it has been suggested that the effects of future climate change on species loss will be small compared with the more direct effects of human factors such as deforestation and hunting (Whitmore 1998). Overall, it appears that climate change may have some important effects on the orangutan and its habitat, but the impact of the inevitable encroachment of humans into their habitat must not be discounted.

3.1.6 Human population growth and predictive models

Direct anthropogenic factors will continue to have a dramatic effect on global biodiversity; therefore it is important to include human effects in predictive models. Bioclimate envelope models have been developed that include current land cover data (Pearson et al. 2004, del Barrio et al. 2006, Luoto et al. 2007). However, predicting the spatial distribution and extent of future land cover change is extremely difficult, particularly over a large area. Human population density has been incorporated into a species distribution model predicting the current range of the flat-headed cat, *Prionailurus planiceps* (Wilting et al. 2010), but has yet to be included in a climate envelope model of the future. In contrast, human factors have been included in a time budget model, predicting the future distribution of the gelada (Dunbar 1998). In this model, the effect of climate change on agriculture was considered, as rising temperatures are likely to shift the region of cultivatable land to higher altitudes, encroaching on gelada habitat. This study also discusses the probable effects of human population growth, although this variable was not included in the modelling process (Dunbar 1998).

Thus, human factors have not yet been widely incorporated into predictive models. This is likely to be a result of limited data availability and the difficulty in accurately projecting these variables into the future. However, in the previous chapter human population density was successfully incorporated into a time budget model for the orangutan. Human population growth has also been predicted for the future (Nakicenovic et al. 2000) and this will be incorporated into the model investigating the future distribution of the orangutan.

3.1.7 Chapter aims

1. To predict the effect of climate change and human population growth on the future distribution of the orangutan and to identify areas where the orangutan has the greatest chance of survival in the future.
2. To determine the relative importance of climate change and human population growth in restricting future distribution patterns. This will highlight which of the two factors poses the greatest threat to the future survival of the orangutan.
3. To predict the effect of climate change on the behaviour and sociality of the orangutan. This will highlight the way in which the orangutan can be expected to alter its behaviour in response to climate change.

3.2 Methods

3.2.1 Future climate data

Predicted climate data for 2080 (the date furthest in the future for which data are available) were downloaded from the International Centre for Tropical Agriculture (Ramirez and Jarvis 2008). Two future climate scenarios were chosen (SRES A2a and SRES B2a), representing alternative predictions for the future. The A2a scenario describes a world characterised by high energy requirements and continuous human population growth. In contrast, the B2a scenario is based on assumptions of lower energy requirements and slower population growth (Nakicenovic et al. 2000).

Within these scenarios, data were available from four different Global Circulation Models: CCCMA-CGCM2 (hereafter CCCMA), CSIRO-MK2 (hereafter CSIRO), HACCPR HadCM3 (hereafter HadCM3) and NIES99, for each of the two scenarios. The CCCMA model was created by the Canadian Centre for Climate Modelling and

Analysis, the CSIRO model by the Commonwealth Scientific and Industrial Research Organisation in Australia, the HadCM3 model by the Hadley Centre at the UK Meteorological Office and the NIES99 model by the National Institute for Environmental Studies in Japan. Models from all four climate centres have been widely used in previous studies of future species distributions: CCCMA (Leng et al. 2008, Peterson 2009, Rödder et al. 2010, Rödder and Schulte 2010, Jenkins et al. 2011, Ihlow et al. 2012); CSIRO (Araujo et al. 2006, Rödder et al. 2010, Rödder and Schulte 2010, Adams-Hosking et al. 2011, Ihlow et al. 2012); Hadley centre (Peterson et al. 2002, Miles et al. 2004, Araujo et al. 2006, Levinsky et al. 2007, Virkkala et al. 2008, Peterson 2009, Rödder et al. 2010, Rödder and Schulte 2010, Virkkala et al. 2010, Ihlow et al. 2012); NIES99 (Rödder and Schulte 2010, Ihlow et al. 2012).

Future climate data were obtained for all four models in order to examine a range of future predictions (Jenkins et al. 2011). All models predict warming climates, while predictions for precipitation vary, with CCCMA predicting a decrease in annual rainfall across Borneo and Sumatra and the other three models predicting increases (Table 3.1). Predicted changes of the eight model/emissions scenario combinations are similar when focussing only on the areas where the orangutan is currently known to live (Table 3.2).

Table 3.1: Changes in mean annual temperature and precipitation predicted across Borneo and Sumatra under the eight combinations of four climate models and two emissions scenarios

	Change in mean annual temperature by 2080 (°C)		Change in mean annual precipitation by 2080 (mm)	
	A2a	B2a	A2a	B2a
CCCMA	+ 2.51	+ 1.60	- 197.12	- 143.46
CSIRO	+ 3.20	+ 1.99	+ 352.17	+ 270.65
HadCM3	+ 3.47	+ 3.04	+ 183.40	+ 176.24
NIES99	+ 3.48	+ 2.19	+ 288.23	+ 88.68

Table 3.2: Changes in mean annual temperature and precipitation predicted across the current range of the orangutan under the eight combinations of four climate models and two emissions scenarios

	Change in mean annual temperature by 2080 (°C)		Change in mean annual precipitation by 2080 (mm)	
	A2a	B2a	A2a	B2a
CCCMA	+ 2.56	+ 1.62	- 181.44	- 152.35
CSIRO	+ 2.59	+ 1.97	+ 402.23	+ 340.33
HadCM3	+ 2.93	+ 2.13	+ 117.12	+ 118.15
NIES99	+ 3.52	+ 2.61	+ 260.85	+ 44.04

3.2.2 Statistical downscaling

The four selected models produce predictions at very coarse resolutions (CCCMA = 3.7° by 3.7°; CSIRO = 5.6° by 3.2°; HadCM3 = 2.5° by 3.75°; NIES99 = 5.6° by 2.8°), which makes it difficult to determine impacts on biodiversity over small areas (Mearns et al. 2003, Ramirez and Jarvis 2008). The area under investigation in this study (the current range of the orangutan) is relatively small, and would therefore comprise a very small number of cells under this coarse resolution. Furthermore, the region is relatively heterogeneous, with large sections adjacent to the coasts or to high altitude areas. As Global Circulation Model predictions take averages over large areas, they are not as accurate over heterogeneous landscapes (Wilby et al. 2004). There are two commonly used methods of obtaining higher resolution regional predictions: regional climate models and statistical downscaling. In this study, statistical downscaling was selected, as regional climate models require a substantial investment of computing resources and so this was not a viable option (Benestad 2004, Schmidli et al. 2006). In contrast, statistically downscaled data are freely available from CIAT (Ramirez and Jarvis 2008). In addition, these statistically downscaled data have been used effectively in numerous

species distribution models to date (Mulligan et al. 2010, Rödder and Schulte 2010, Heubes et al. 2011, Jenkins et al. 2011, Laderach et al. 2011, Ihlow et al. 2012).

3.2.3 Future human population density data

The human population density in 2080 across the region was predicted by calculating the percentage increase in global population from 2008 to 2080 predicted by the two emissions scenarios. The population density of each pixel was then increased by the same percentage (an increase of 98% under the A2a scenario and 43% under the B2a scenario).

3.2.4 Model procedure

The time budget model was run using future climate data from all four models (CCCMA, CSIRO, HadCM3 and NIES99) under both emissions scenarios (SRES A2a and B2a) yielding eight sets of results in total. The future climate data were available at a slightly lower resolution than the rest of the data used in the model building process (0.000897° vs 0.000833°). All data were therefore resampled to a common pixel size (0.000897°). Because very little is known about the effect of climate change on tropical forests (Clark 2004), forest cover was assumed to remain constant between now and 2080. Similarly, land cover data were maintained as in the original model, as detailed data with which to build a land cover change sub-model were not available over the large area modelled in this study.

The regression equations were implemented in ArcGIS using the climate data from each model/emissions scenario combination to predict the amount of time that orangutans would need to devote to each time budget component in the future. From this, future maximum ecologically tolerable group sizes could be calculated, and the climatically

determined future distribution predicted. Raster cells with an unsuitable land cover category under current conditions were classed as unsuitable for orangutan habitation in the future, as much of this land is agricultural and so it is unlikely that these habitats will become forested again in the future. Future human population density data were then incorporated into the model, and all cells with HPD greater than 20 per km² classed as unsuitable, as in the original model.

3.2.5 The extent and causes of range loss

As orangutans are already endangered and numbers continue to decline, it seems extremely unlikely that they will be able to extend their range into newly suitable regions in the future, as populations are unlikely to increase in size and range. In particular, as the orangutan has such a slow life history, increases in population size will occur at an extremely slow rate. In addition, as much of the land in Borneo and Sumatra has already been deforested and converted to plantations or agricultural land, even if the changing climate makes these areas climatically suitable for the orangutan, they are unlikely to be left to regenerate into suitable forest habitat. Analyses were therefore restricted to the effects of climate change on the areas where the orangutan was correctly predicted to survive today.

The model predictions were examined to determine the percentage of the orangutan's current range that is predicted to become unsuitable under the different future scenarios. Current range here refers to the areas that were correctly predicted to be suitable using the time budget model. Including the areas that were predicted to be unsuitable, but where the orangutan is currently known to survive could lead to incorrect values for the predicted range reduction. Thus, for all analyses in this chapter, only the regions that

were correctly predicted to be suitable habitat using the time budget model were considered.

The predicted range reduction was investigated further to distinguish the percentage of the range that was classified as unsuitable as a result of climatic changes, and that classified as unsuitable due to increases in human population density. A particular strength of time budget models is that they allow the effects of climate change on behaviour to be explored, and thereby indicate what it is that is making habitat unsuitable for orangutans, i.e. the mechanisms underlying the range reduction. Where predicted range loss was substantial, time budget variables were compared between the present and the future in the areas that were predicted to become unsuitable in the future, to determine which factor caused these areas to become unsuitable.

3.2.6 The effect of climate change on time budget allocations and group size

The strength of time budget models is that they can also provide an indication of the behavioural changes that may be expected to occur in the future. Thus, the effects of climate change on time budgets and group size were examined to determine how these variables may change in the future. These analyses demonstrate only the effect of climate change on behaviour; human population growth was included as a filter and thus does not directly impact on time budget allocations. Hence, the effect of human population growth on future behaviour can not be explored. However, only areas that were predicted to be suitable under the full time budget model (i.e. including the land cover and HPD filter) were investigated, as there is no need to explore behavioural changes in areas where high human impacts will prevent orangutan habitation. Time budget variables were calculated for a constant group size of one so that values could be directly compared between the present and the future. To improve the independence of

the data points used in this analysis, a grid of 374 points across the whole of Borneo and Sumatra (each separated by 0.5° longitude and latitude) was used (hereafter referred to as the grid). Locations on this grid that fell in areas where the orangutan was predicted to survive under both current and future conditions were used. Predicted values for each time budget variable (at a group size of one) and maximum ecologically tolerable group size were compared between the present and the future at these locations using Wilcoxon signed-ranks tests in SPSS (SPSS 2008).

3.3 Results

3.3.1 The effects of climate change and human population growth on the range of the orangutan

The predicted changes to the range of the orangutan under the two emissions scenarios, using the four different climate models are displayed in Figures 3.1-3.8.

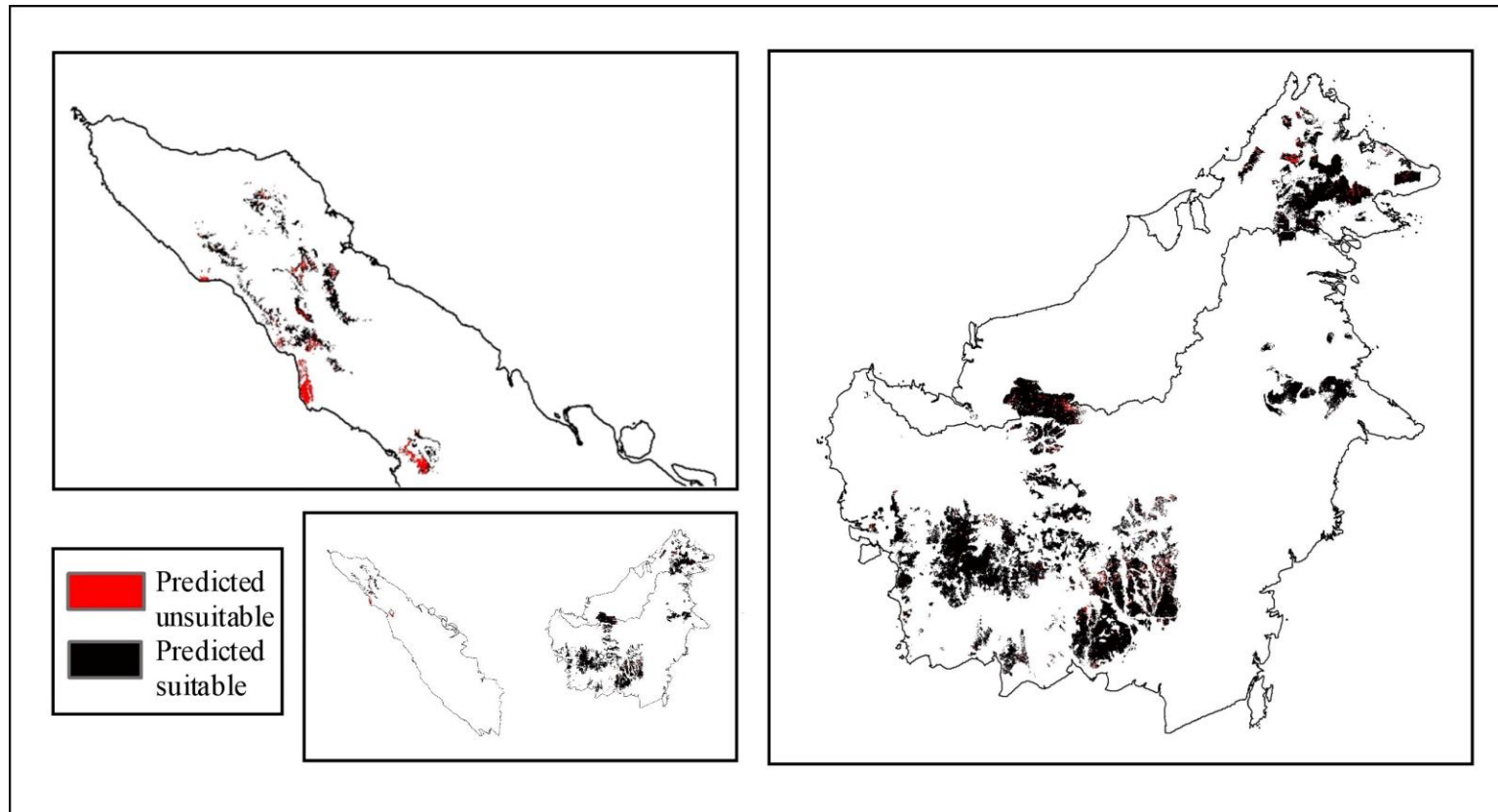


Figure 3.1: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the CCCMA model under the A2a emissions scenario

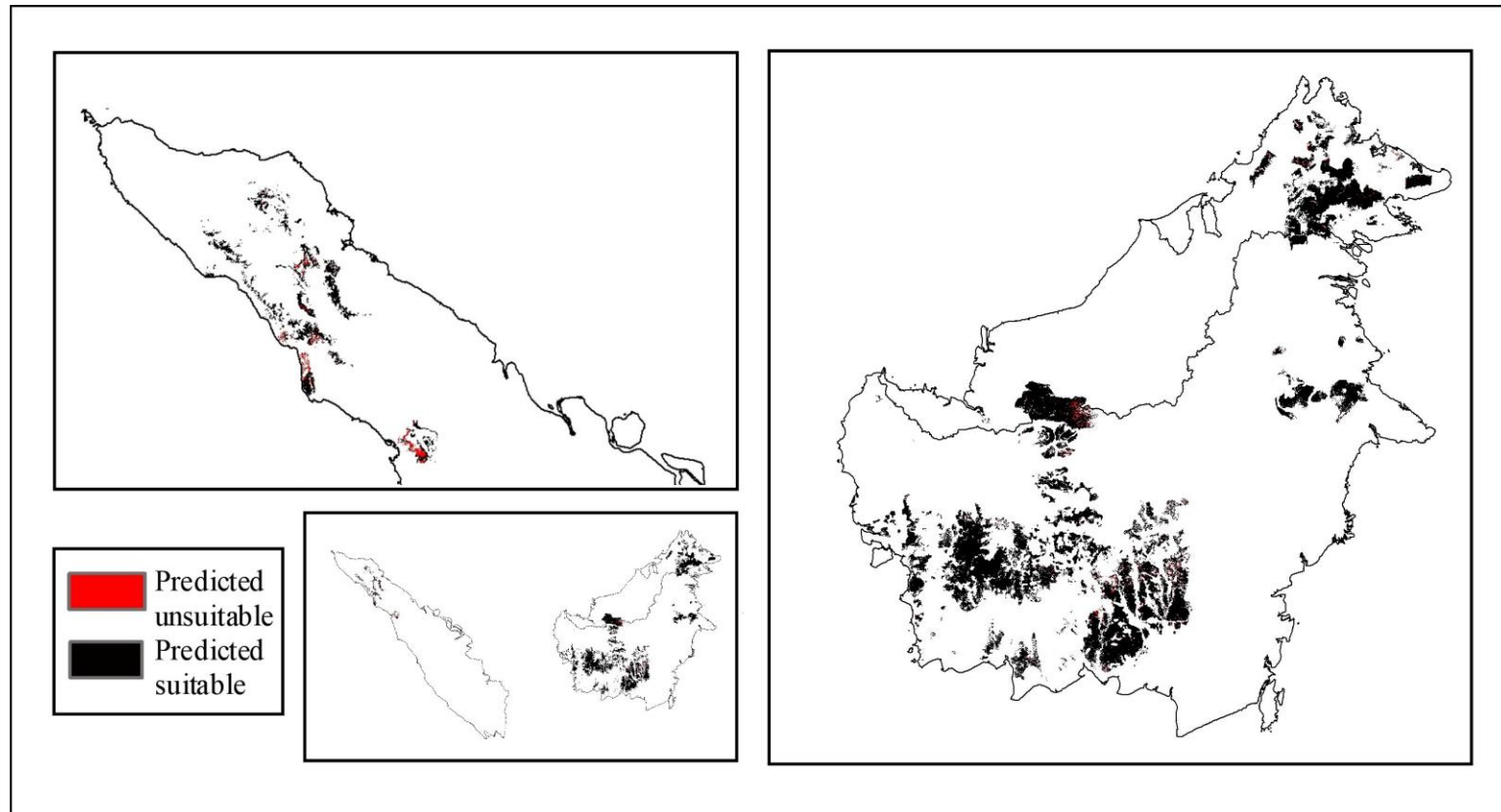


Figure 3.2: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the CCCMA model under the B2a emissions scenario

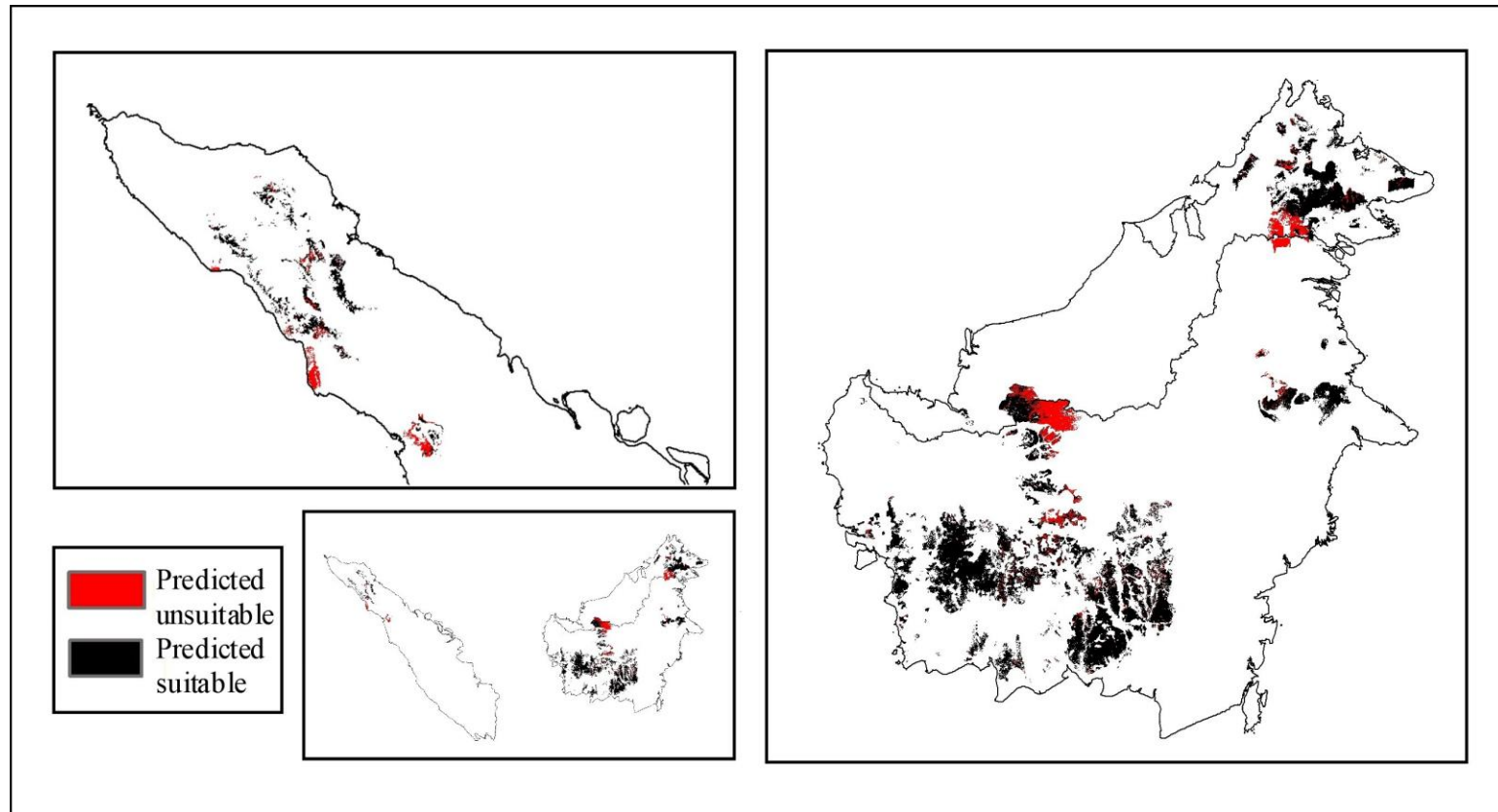


Figure 3.3: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the CSIRO model under the A2a emissions scenario

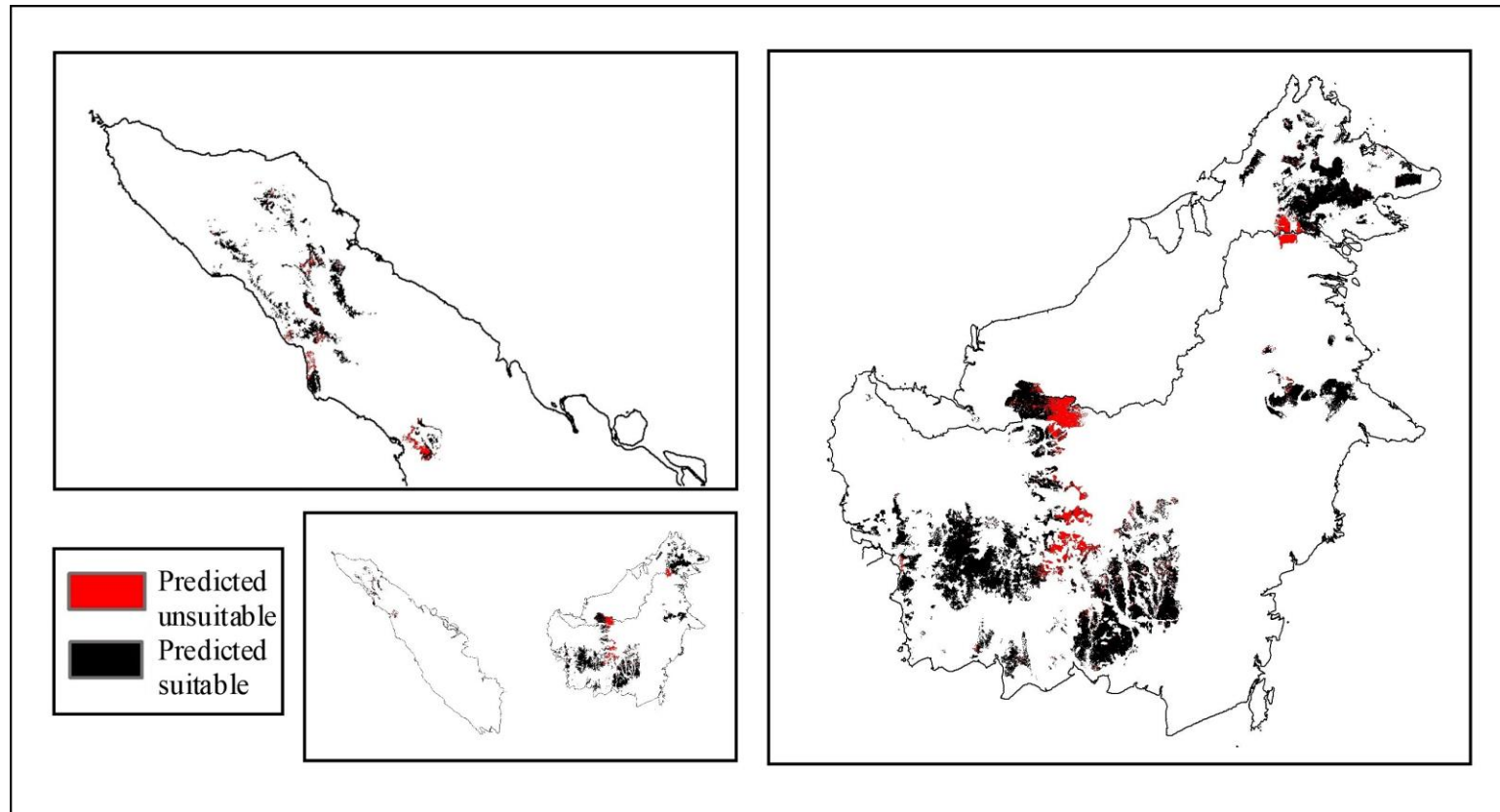


Figure 3.4: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the CSIRO model under the B2a emissions scenario

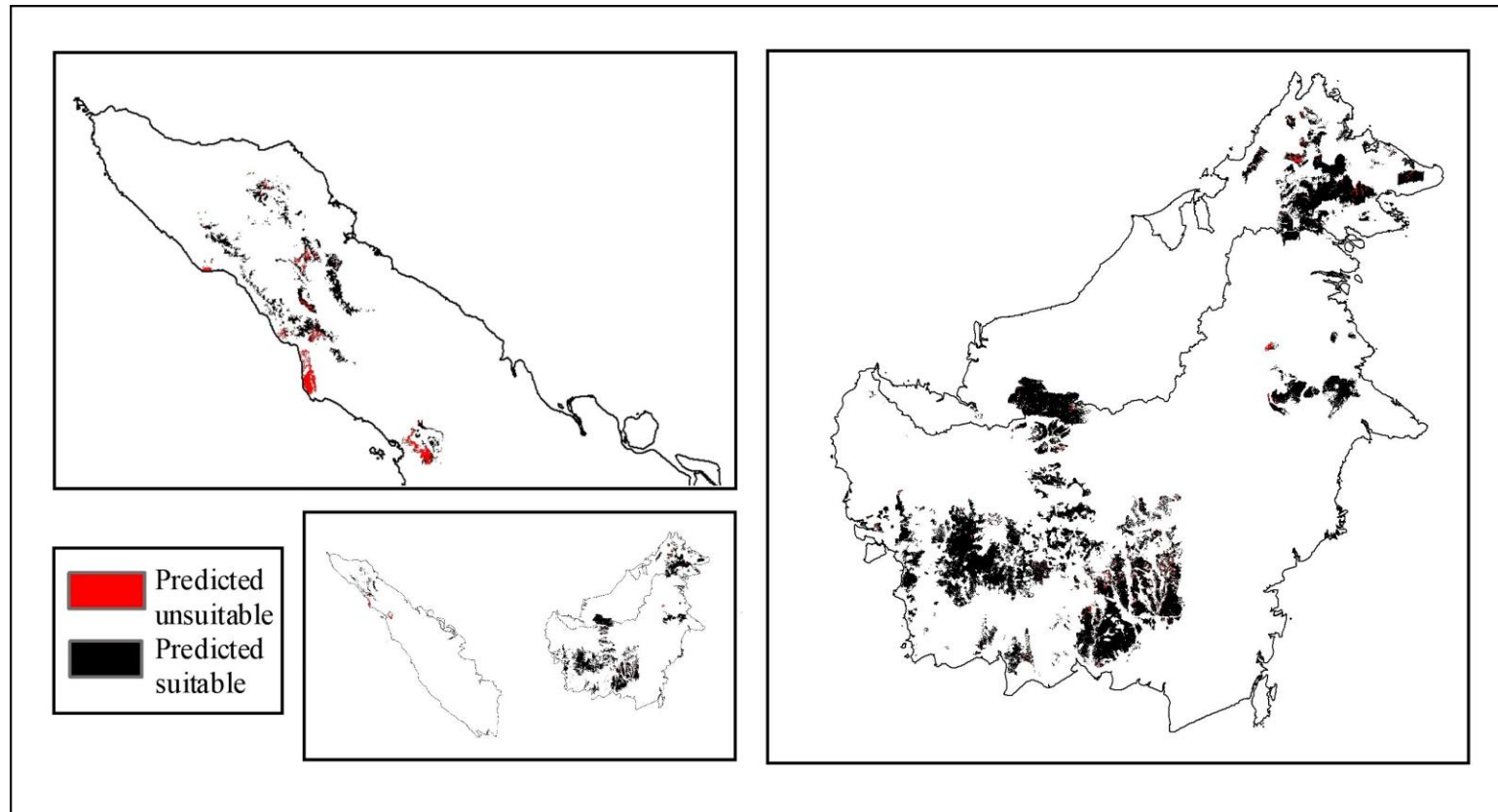


Figure 3.5: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the HadCM3 model under the A2a emissions scenario

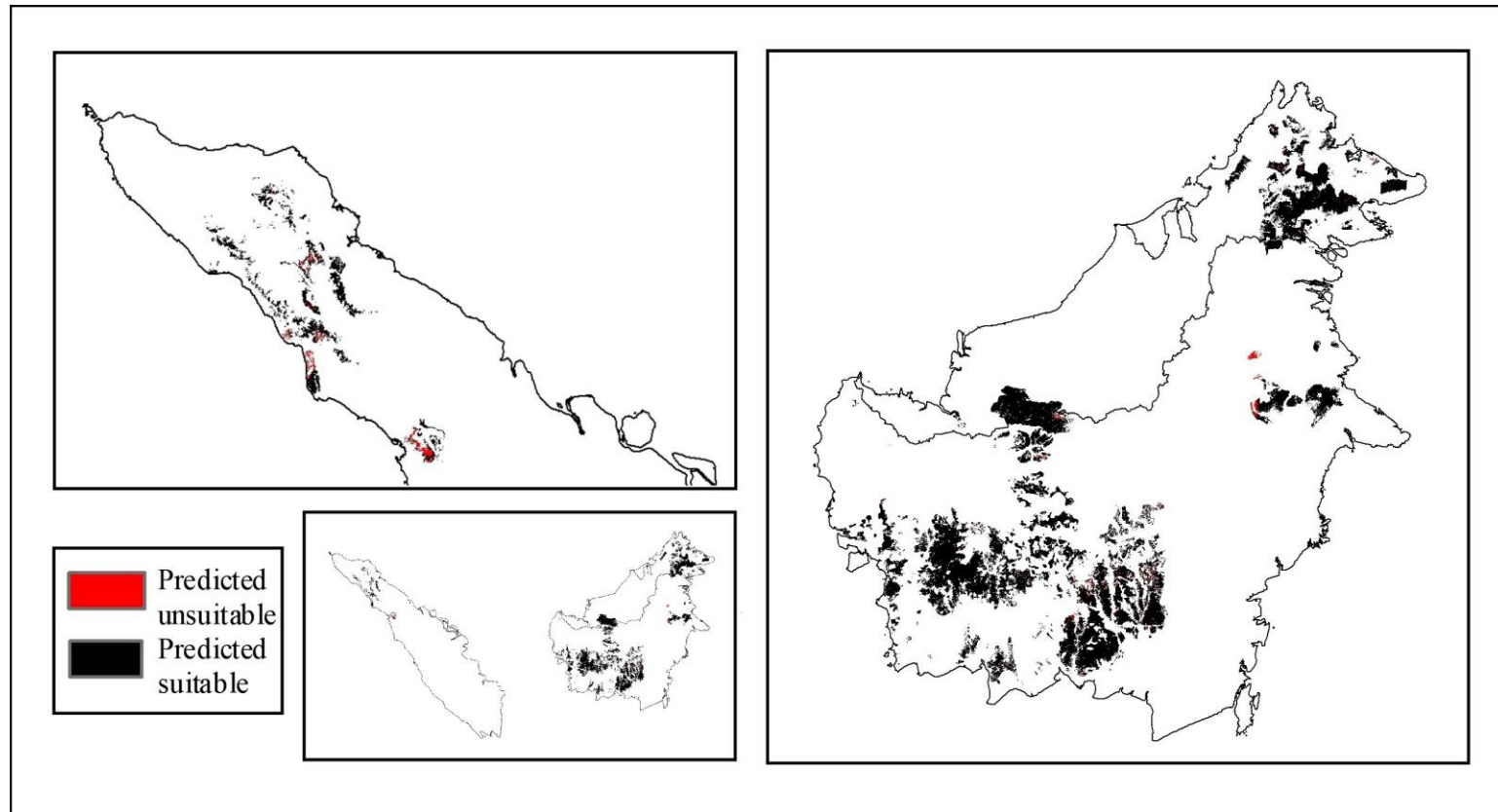


Figure 3.6: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the HadCM3 model under the B2a emissions scenario

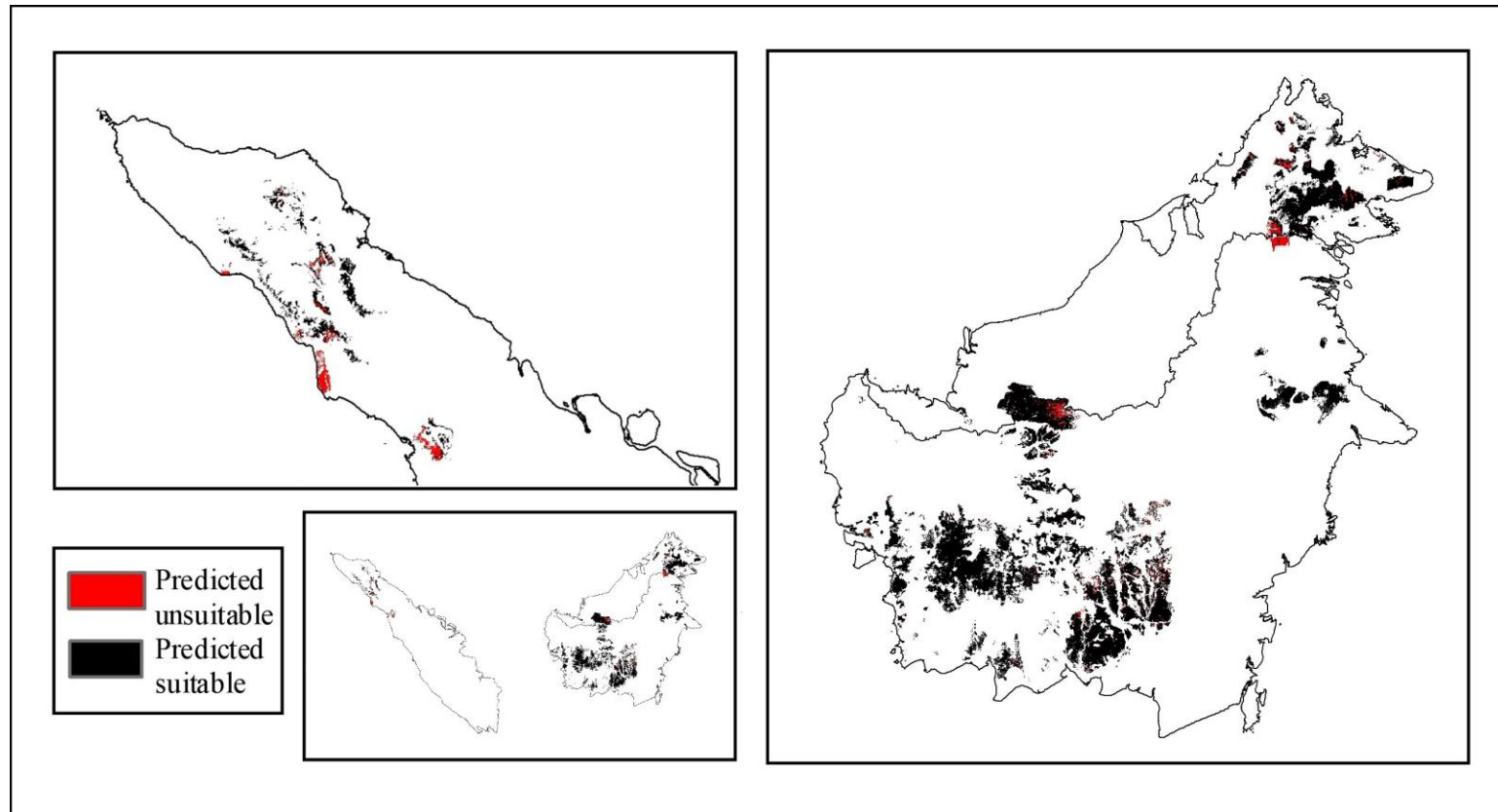


Figure 3.7: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the NIES99 model under the A2a emissions scenario

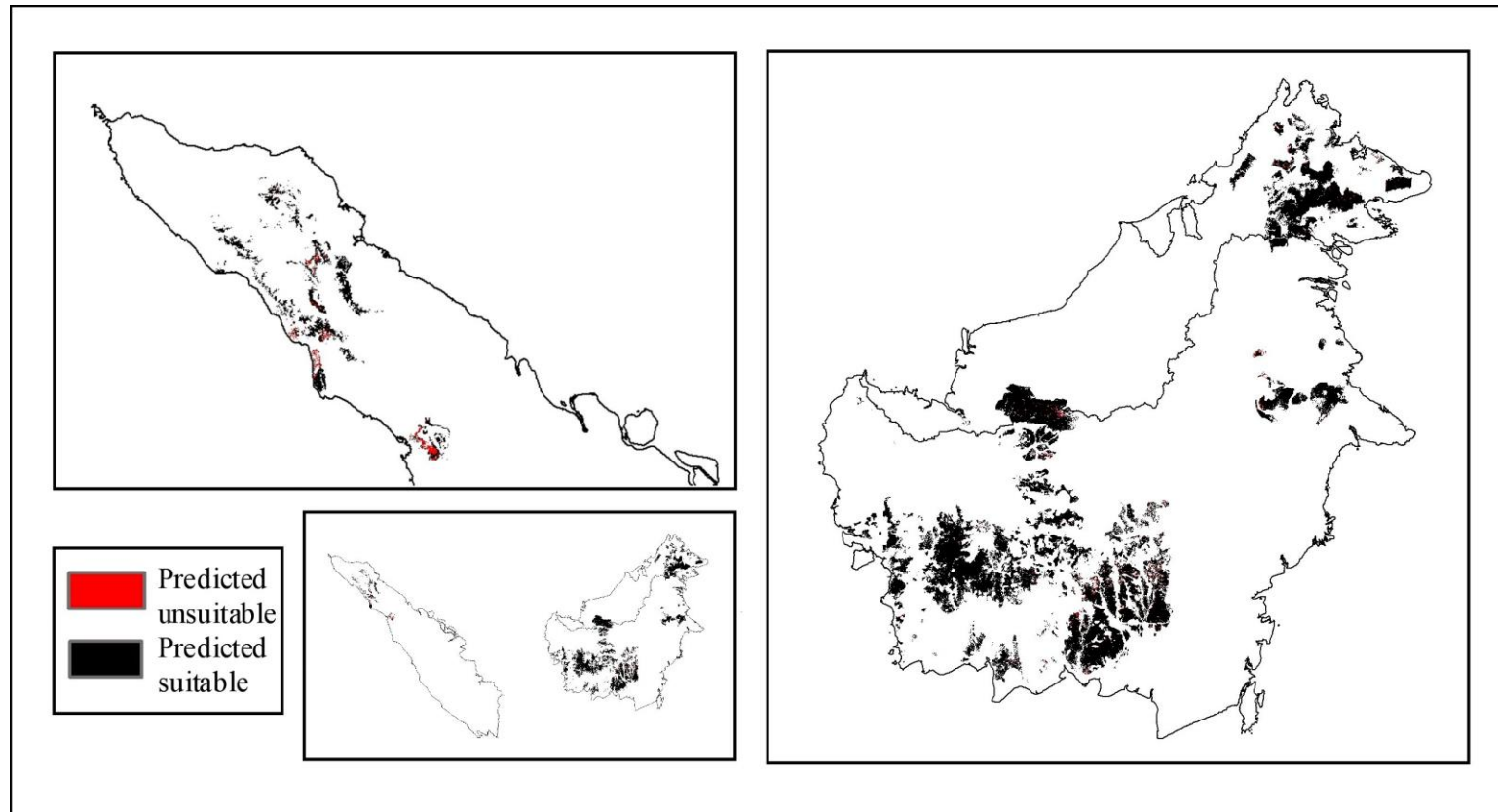


Figure 3.8: Locations within the current range of the orangutan that are predicted to be suitable and unsuitable by the NIES99 model under the B2a emissions scenario

The percentage of the orangutan's current range that is predicted to become unsuitable as a result of climate change and human population growth was calculated (the areas classed as false absences in the original model were excluded) (Table 3.3). The majority of the models predict that the orangutan will lose approximately 5% of its current range under scenario A2a and around 3% under scenario B2a. However, the CSIRO model predicts a larger reduction in the suitable range of the orangutan, by just over 15% under scenario A2a and 13% under scenario B2a. It is clear that under the majority of climate model/emissions scenario combinations, climate change has a very small impact on the range of the orangutan. Only under the NIES99-A2a combination and both CSIRO models does climate change appear to have a strong effect on distribution patterns. Instead, for the majority of models, a large proportion of the range loss can be attributed to the effects of human population growth.

Table 3.3: The percentage of the orangutan's current range that is predicted to be lost as a result of climate change alone, human population growth alone and overall.

	Percentage range lost as a result of climate change		Percentage range lost as a result of human population growth		Total percentage range loss	
	A2a	B2a	A2a	B2a	A2a	B2a
CCCMA	0.84	0.53	4.27	2.76	5.11	3.28
CSIRO	11.09	10.84	4.25	2.60	15.34	13.43
HadCM3	0.28	0.59	4.54	2.76	4.83	3.35
NIES99	2.14	0.28	4.47	2.76	6.61	3.05

3.3.2 *The factors restricting the future distribution of the orangutan under the CSIRO model*

The CSIRO model predicts a much larger range reduction than the other three models under both scenarios, and this is largely attributable to climate change. To investigate which time budget components were most affected, mean time budget values were obtained for the areas predicted to become unsuitable under the CSIRO model, and compared with the mean values in these areas under current conditions (at a group size of one). The mean values for the percentage of fruit in the diet and for feeding time increased considerably by 2080 under both scenarios, with moving time increasing to a lesser degree and resting time changing very little (Figures 3.9 and 3.10).

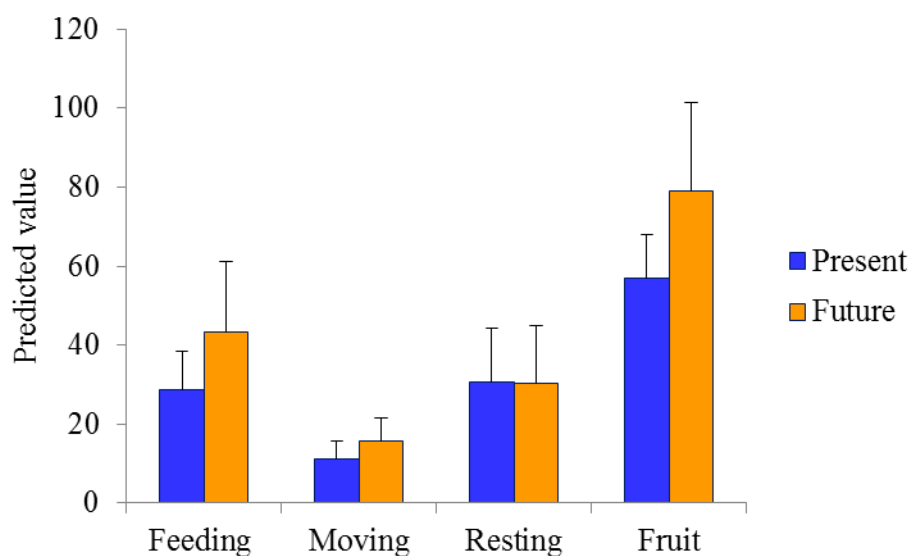


Figure 3.9: The mean (plus standard deviation) of feeding time, moving time, resting time and the percentage of fruit in the diet at a group size of one in the areas predicted to be unsuitable under the A2a scenario using the CSIRO model. Values are presented for these areas both in the present and in the future for comparison.

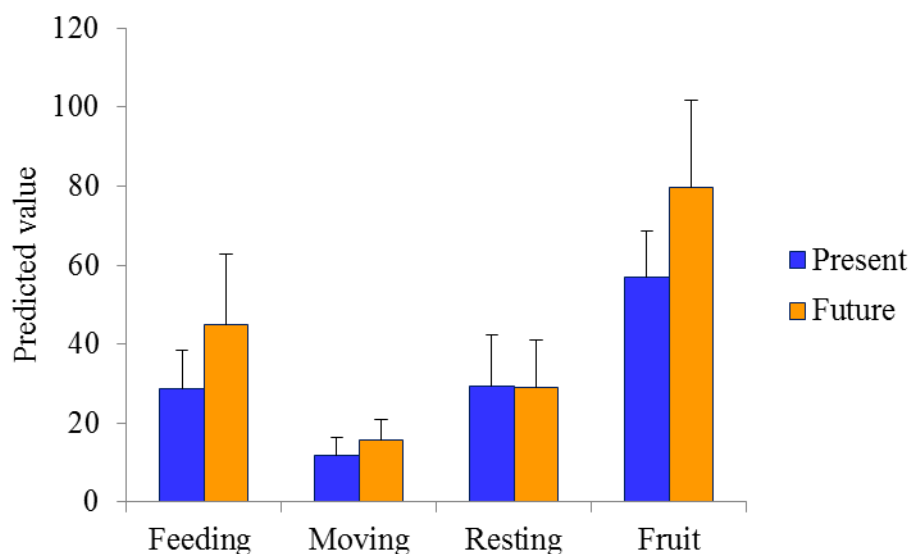


Figure 3.10: The mean (plus standard deviation) of feeding time, moving time, resting time and the percentage of fruit in the diet at a group size of one in the areas predicted to be unsuitable under the B2a scenario using the CSIRO model. Values are presented for these areas both in the present and in the future for comparison.

3.3.3 The effect of climate change on time budget allocations

Time budget estimates were obtained for each of the locations in the grid in which the orangutan was predicted to survive both now and in the future using a group size of one, to compare current and future values. The predicted changes to time budget allocations are displayed in Table 3.4 and Figures 3.11-3.14. Feeding time is only predicted to increase significantly under the B2a scenario by the NIES99 model and the CSIRO model (Figure 3.11). The other model/emissions scenario combinations predict no significant change. Moving time is predicted to increase under both scenarios by the CCCMA and CSIRO models, and under the A2a scenario by the NIES99 model (Figure 3.12). Resting time is predicted to decrease under both scenarios by the CCCMA, HadCM3 and NIES99 models, while the CSIRO model predicts no significant change (Figure 3.13). The percentage of fruit in the diet is predicted to increase under both scenarios by the CSIRO and NIES99 models, and under the B2a scenario by the

HadCM3 model (Figure 3.14). The other model/emissions scenario combinations predict no significant change.

Table 3.4: Results of Wilcoxon signed-ranks tests, indicating the direction and significance of the predicted changes to time budget allocations within locations in which the orangutan is predicted to survive under both current and future climates, for all eight combinations of the four climate models and two emissions scenarios. Bold values indicate that differences are significant.

		A2a				B2a			
		Direction	Z	N	P	Direction	Z	N	P
Feeding	CCCMA	-	-0.983	24	0.326	-	-0.522	24	0.602
	CSIRO	-	-0.742	20	0.458	Increase	-2.185	21	< 0.05
	HadCM3	-	-0.524	24	0.600	-	-0.403	24	0.687
	NIES99	-	-1.689	24	0.091	Increase	-2.142	24	< 0.05
Moving	CCCMA	Increase	-2.621	24	< 0.01	Increase	-2.560	24	< 0.05
	CSIRO	Increase	-4.054	20	< 0.001	Increase	-4.055	21	< 0.001
	HadCM3	-	-0.017	24	0.986	-	-0.281	24	0.779
	NIES99	Increase	-4.082	24	< 0.001	-	-0.137	24	0.891
Resting	CCCMA	Decrease	-3.662	24	< 0.001	Decrease	-2.784	24	< 0.01
	CSIRO	-	-0.829	20	0.407	-	-1.269	21	0.204
	HadCM3	Decrease	-4.018	24	< 0.001	Decrease	-3.949	24	< 0.001
	NIES99	Decrease	-3.742	24	< 0.001	Decrease	-4.019	24	< 0.001
Fruit	CCCMA	-	-0.599	24	0.549	-	-0.750	24	0.453
	CSIRO	Increase	-2.507	20	< 0.05	Increase	-2.714	21	< 0.01
	HadCM3	-	-1.383	24	0.167	Increase	-2.001	24	< 0.05
	NIES99	Increase	-2.360	24	< 0.05	Increase	-2.618	24	< 0.01

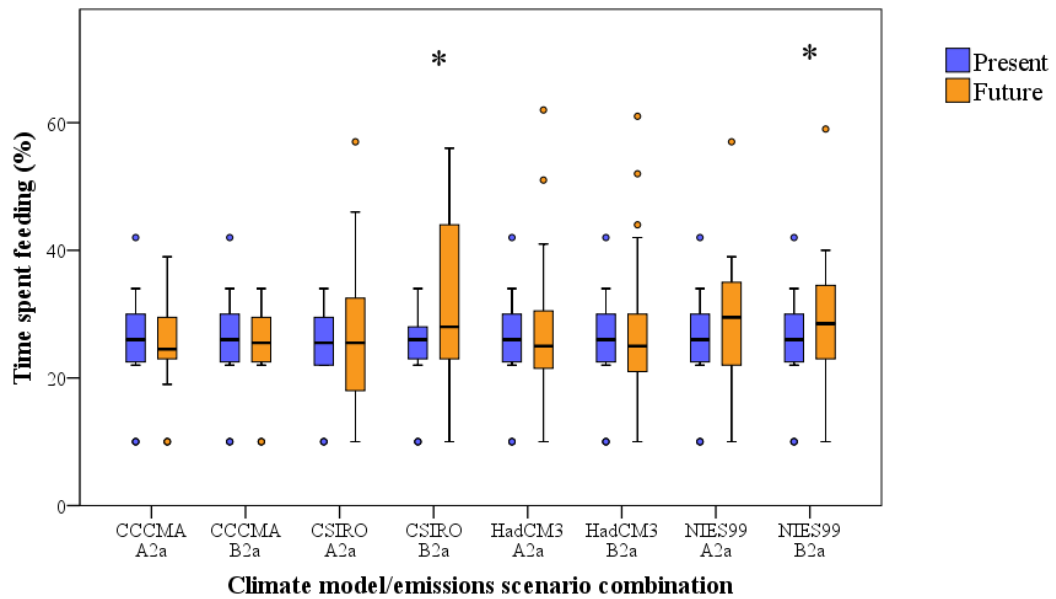


Figure 3.11: Boxplots of the percentage of time spent feeding at a group size of one under both present and future climatic conditions for all eight combinations of the four climate models and two emissions scenarios. Only the locations in which the orangutan is predicted to survive under both the current and the future climates were included. (Dots signify outliers and * indicates that $P < 0.05$).

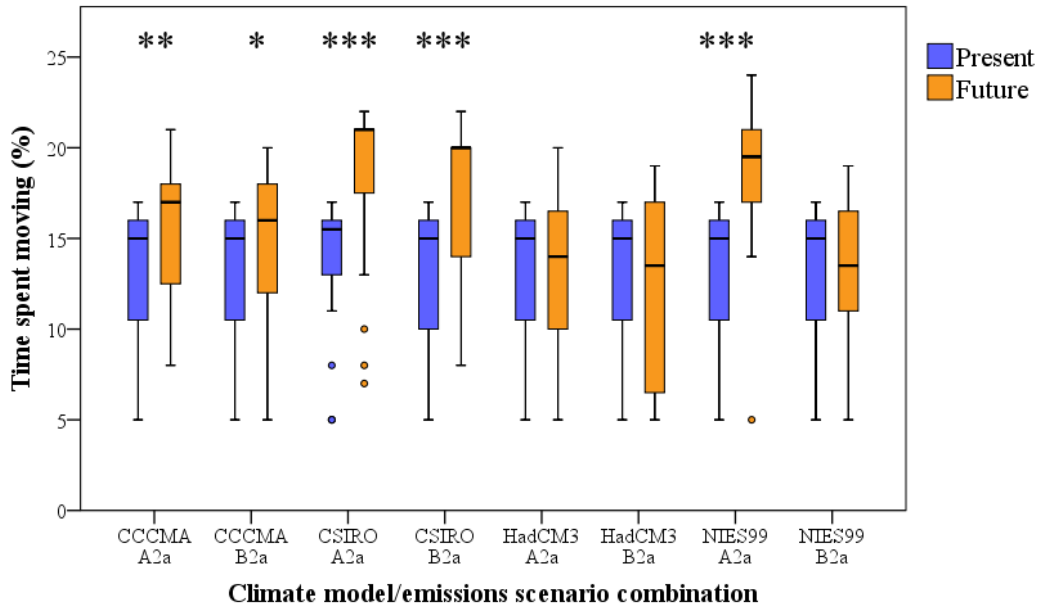


Figure 3.12: Boxplots of the percentage of time spent moving at a group size of one under both present and future climatic conditions for all eight combinations of the four climate models and two emissions scenarios. Only the locations in which the orangutan is predicted to survive under both the current and the future climates were included. (Dots signify outliers, * indicates that $P < 0.05$, ** indicates that $P < 0.01$ and *** indicates that $P < 0.001$).

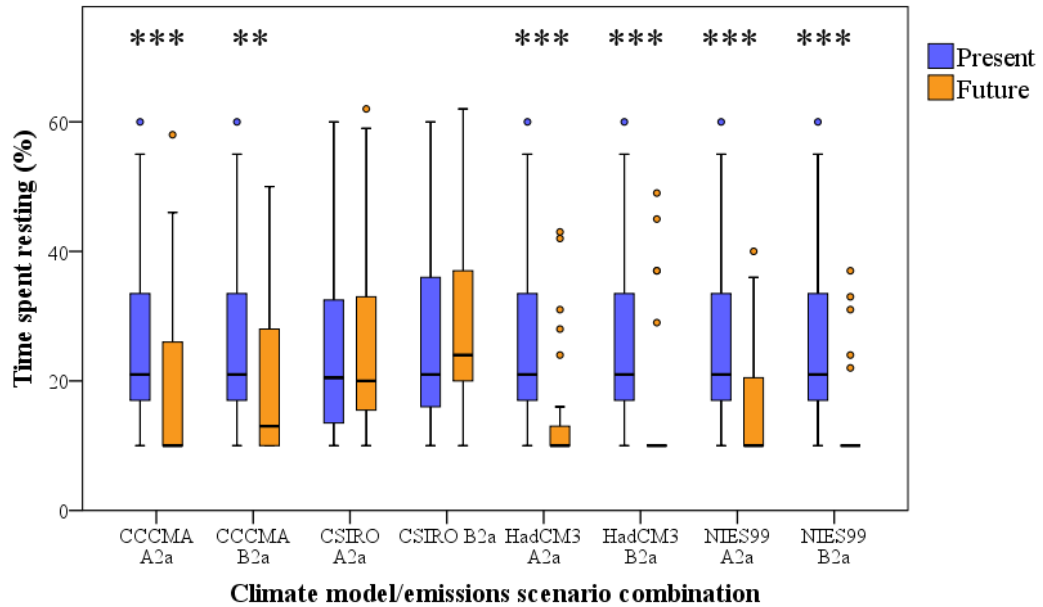


Figure 3.13: Boxplots of the percentage of time spent resting at a group size of one under both present and future climatic conditions for all eight combinations of the four climate models and two emissions scenarios. Only the locations in which the orangutan is predicted to survive under both the current and the future climates were included. (Dots signify outliers, ** indicates that $P < 0.01$ and *** indicates that $P < 0.001$).

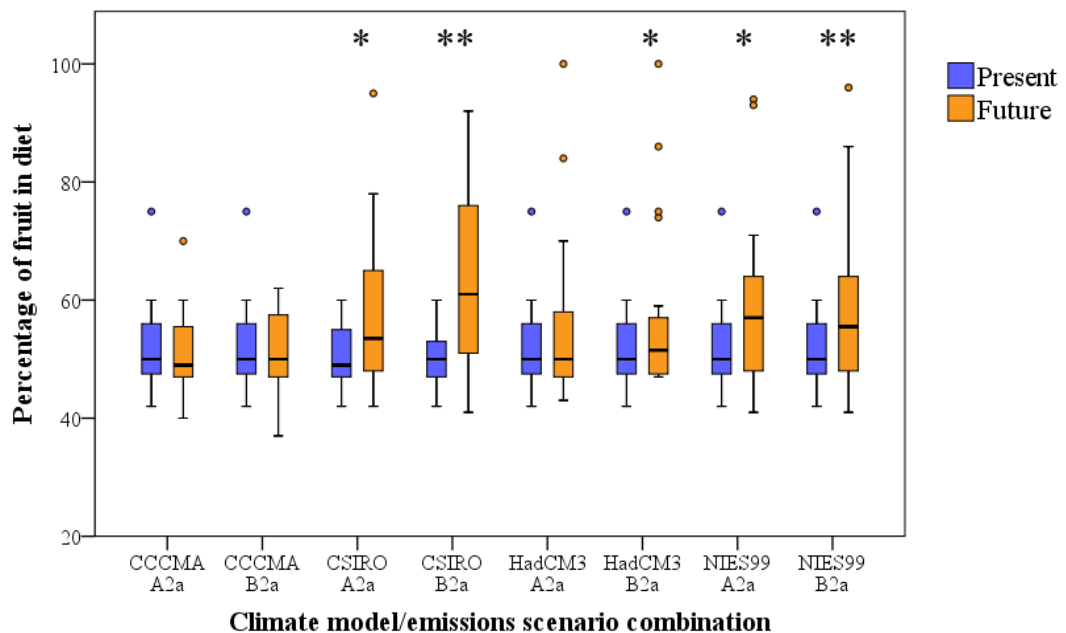


Figure 3.14: Boxplots of the percentage of fruit in the diet at a group size of one under both present and future climatic conditions for all eight combinations of the four climate models and two emissions scenarios. Only the locations in which the orangutan is predicted to survive under both the current and the future climates were included. (Dots signify outliers, * indicates that $P < 0.05$ and ** indicates that $P < 0.01$).

3.3.4 The effect of climate change on maximum ecologically tolerable group size

Maximum ecologically tolerable group size estimates were also compared within the locations where the orangutans were predicted to survive under both current and future climates. For each model/emissions scenario combination as well as the original model, predicted values were obtained for all points on the grid in which the orangutan was predicted to survive under both climatic conditions. These values were compared to determine the effect of climate change on maximum ecologically tolerable group size. All of the models except CSIRO predicted either no significant change or an increase in the maximum ecologically tolerable group size (Table 3.5 and Figure 3.15). The CSIRO model predicted a decrease in the maximum ecologically tolerable group size in the future.

Table 3.5: Results of Wilcoxon signed-ranks tests, indicating the direction and significance of predicted changes to the maximum ecologically tolerable group size within locations in which the orangutan is predicted to survive under both current and future climates, for all eight combinations of the four climate models and two emissions scenarios. Bold values indicate that differences are significant.

	A2a				B2a			
	Direction	Z	N	P	Direction	Z	N	P
CCCMA	Increase	-2.560	24	< 0.05	-	-1.958	24	0.050
CSIRO	Decrease	-2.820	20	< 0.01	Decrease	-3.382	21	< 0.01
HadCM3	Increase	-3.193	24	< 0.01	Increase	-3.052	24	< 0.01
NIES99	-	-0.281	24	0.779	Increase	-3.279	24	< 0.01

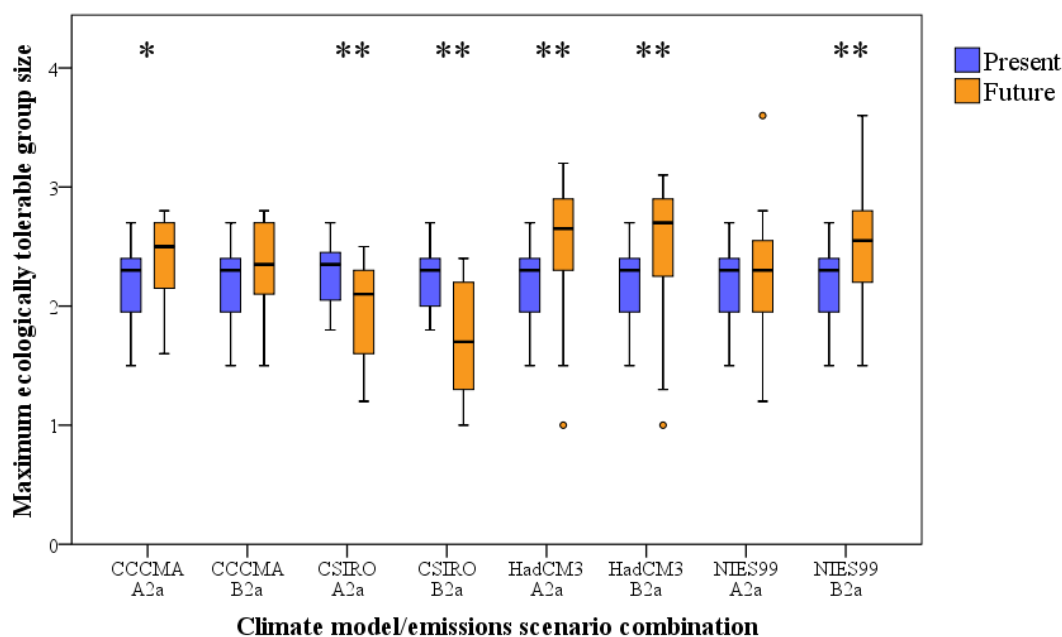


Figure 3.15: Boxplots of maximum ecologically tolerable group size under both present and future climatic conditions for all eight combinations of the four climate models and two emissions scenarios. Only the locations in which the orangutan is predicted to survive under both the current and the future climates were included. (Dots signify outliers, * indicates that $P < 0.05$ and ** indicates that $P < 0.01$).

3.4 Discussion

A time budget model was used to predict the effect of climate change and human population growth on the behaviour and distribution of the orangutan. The results showed that moving and feeding time demands may become more severe in the future, while resting time may become less restrictive. Only one of the climate models tested predicted a substantial change in the distribution of the orangutan, while a relatively mild effect on the range of the orangutan was found for the remaining three models. However, given the additional pressures of deforestation and the less direct effects of climate change that could not be incorporated into the model, even this relatively small reduction could have a severe impact on the survival of the species. Human population growth was predicted to have a greater impact on distribution patterns than the climate

under the majority of the models, emphasising the importance of anthropogenic factors in determining the future survival of these species.

3.4.1 The predicted effects of climate change and human population growth on the range of the orangutan

Under most of the scenarios tested, climate change and human population growth were predicted to have a relatively mild effect on orangutan distribution patterns. The current range of the orangutan will most likely not contract considerably, with a reduction of between 3 and 7% predicted by three out of four climate models. The exception is the CSIRO model, which predicts a much larger range reduction under both scenarios (around 15% under A2a and 13% under B2a). Although the generally low range reductions predicted by the models could be interpreted as an encouraging result, it is important to note that the models may be seriously underestimating the effects of both climate change and human population growth on the orangutan, as a number of important variables could not be incorporated such as food quality, future forest cover and the effects of extreme events such as those caused by El Niño as a result of a lack of available data on these variables. Investigating these variables and relationships in more detail so that they can be predicted for the future would be an important extension to this study, but was beyond the scope of this thesis.

The possible effects of climate change on the energy content of orangutan food sources, which may be strongly affected by temperature, rainfall and carbon dioxide levels (Coley 1998, Schuur 2003, Clark 2004), were not included. Changes to the percentage of forest cover were also not incorporated into the model as the response of tropical forests to climate change is extremely uncertain (Clark 2004). It is possible, however, that the increased temperatures could lead to considerable forest dieback (Bonan 2008,

Allen et al. 2010). The percentage of forest cover was found to be an important variable in the time budget model; therefore if climate change causes strong negative effects on forest cover, this could destroy the remaining orangutan habitat, with disastrous consequences for surviving populations. Furthermore, the effect of future deforestation was not incorporated in the model. Sumatra and Borneo have both experienced dramatic forest loss over the past decade, particularly the eastern lowlands of Sumatra and the peatlands of Sarawak, which lose around 5% of forest per year (Miettinen et al. 2011a). This pattern shows no signs of abating; therefore further deforestation is likely to play a considerable role in determining the future of the orangutan. Indeed, Sala et al. (2000) predict that by 2100 there will be dramatic reductions in tropical forest area, largely as a result of changing land use. Assuming the continuation of past trends, forest cover in Borneo may be reduced to less than a third of the island by 2020 (Rautner et al. 2005). Lowland areas, which provide high quality orangutan habitat, are particularly vulnerable to exploitation as they are highly accessible (Linkie et al. 2004, Campbell-Smith et al. 2011a). In Bukit Barisan Selatan National Park, Sumatra, for example, it has been predicted that by only 2036 all of the lowland forest habitat will have been eliminated (Kinnaird et al. 2003). Future research is needed that includes both the effect of climate change on forest cover as well as deforestation projections to provide a broader picture of the future distribution of the orangutan.

The effect of extreme events caused by the El Niño Southern Oscillation was also not specifically incorporated in the model. The time budget model focusses on overall habitat suitability based on average conditions, while El Niño events are short periods of extreme conditions which may lead to sudden extinctions. Although the effect of El Niño on average temperature and rainfall is included in the future climate data used in the model (Solomon 2007), the more immediate effects of extreme weather events that

occur as a result of this system cannot be included in a time budget model. El Niño events tend to occur every two to seven years and last for a period of 12 to 18 months (Dawson et al. 2002). This leads to drought in South-east Asia which is thought to stimulate the mast fruiting events that are unique to lowland dipterocarp forests, in which a vast number of trees produce huge quantities of fruit and flowers simultaneously, both satiating seed predators and increasing pollination activity (Sakai 2001, Sakai et al. 2006). During these mast fruiting events orangutans gorge on fruit, maximising their intake of calories (Knott 1998). Orangutans store these excess calories as fat, which helps them to survive the subsequent lean period (Wheatley 1982, Knott 1998). The high fruit production characteristic of mast fruiting events consumes the stored reserves of the trees, which limits subsequent fruit production (Wright et al. 1999, Holmgren et al. 2001). If two dry years occur in succession, dipterocarps are therefore not able to fruit heavily in the second year (Whitmore 1998).

Orangutans appear to have successfully adapted to this unusual fruiting pattern, by building up large fat stores and relying on these to survive until the next fruiting event. However, since the middle of the 1970s the frequency and intensity of El Niño has been unusually high compared with the previous 100 years (Solomon 2007). It therefore seems likely that in the future El Niño events will occur both more frequently and with greater intensity (Dawson et al. 2002, Charrette et al. 2006, Solomon 2007). If this leads to more frequent mast fruiting events, the trees may not have time to rebuild their energy stores to a level for sufficient fruiting. This will impact not only the animals that rely on the fruit for survival, but also the reproductive success of the trees. Logging is likely to exacerbate this problem, by further reducing the extent and intensity of mast fruiting (Curran et al. 1999). There is evidence that these effects are already being felt. At Gunung Palung, for example, during three mast fruiting events in eight years, more

than 48 species of canopy trees failed to produce adequate seedling regeneration (Curran et al. 1999). The probable increase in the frequency and intensity of El Niño therefore poses a serious threat to the survival of both the South-east Asian forests and their frugivores. The effects on the frugivorous species are likely to be particularly dramatic as a single year of extreme weather could lead to the failure of numerous tree species to fruit, leading to famine and the widespread death of individuals dependent on the fruit to survive (Corlett and Lafrankie 1998). As orangutans have an extremely slow life history, it would take populations a very long time to recover from such events.

The predicted changes to the El Niño cycle are also likely to have a significant effect on the frequency and severity of forest fires. In 1997 and 1998, for example, an El Niño drought led to intense forest fires across Borneo. In East Kalimantan alone, 5.2 million hectares of land burned in the largest forest fires ever to occur in the region (Siegert et al. 2001). An estimated 1,000 out of the 40,000 orangutans in Kalimantan were killed in these fires (Suhud and Saleh 2007), and almost the whole of Kutai National Park was burned in just a few days (Cleary 2008). Unfortunately, this was not an isolated event, as devastating fires raged across Indonesia in both 2002 and 2006; indeed these years rank amongst those with the highest rate of forest fires in Indonesia's history (Ardiansyah, 2009). The increase in fire, however, cannot be entirely attributed to the changing El Niño patterns. Land clearance, which has occurred at such a dramatic rate in both Borneo and Sumatra, increases fire danger by producing dead, flammable material, opening the canopy thereby allowing understory vegetation to grow, and letting in wind which dries out the dead material and helps fires to spread (Dawson et al. 2002). The fires in 1997 and 1998 were more severe in logged areas than undisturbed forests and the impact of the fires was negatively correlated with the time elapsed since the logging occurred (Siegert et al. 2001). There is therefore a clear synergism between

the effects of El Niño and logging which could prove devastating for the forests through their influence on fire. This factor is not one that could be included in the model; however, it is important to highlight, as fire has the potential to destroy the remaining populations of orangutans and their habitat.

Synergistic effects such as these, between humans and the climate, are of particular concern and are very difficult to predict. Rising sea levels in response to higher global temperatures, for example, will lead to a reduction in land for both agriculture and for human settlement (Measey 2010). Altered climates may also reduce the suitability of current agricultural land (Dunbar 1998), leading to further pressure on the remaining tropical rainforests. As the orangutan is already constrained to very limited areas of remaining forest, this could decimate surviving populations.

Despite the unpredictable nature of such variables, the time budget model produces the first indication of the effect that climate change and human population growth might have on the overall distribution of the orangutan. It is interesting that for the majority of the models range reductions were largely in response to the increase in human population density as opposed to the changing climates. This indicates that the orangutan may be able to survive under a range of climates, and that if the climate remains within the range of the three less severe models, the orangutan should not experience a dramatic reduction in suitable habitat as a direct result of climatic changes. These results are in accordance with previous models of tropical regions, which predict that the major influence on the future of these ecosystems will be anthropogenic (Sala et al. 2000, Lucht et al. 2006). In the only previous study using a modelling approach to explore the future of the orangutan, Gregory et al. (2012) found that in Sabah, land cover changes would have a greater impact than climate change. This study predicted that climate change may lead to a reduction in orangutan abundance in the eastern

forests, and an increase in habitat suitability in the west, but did not suggest that any of the orangutan range in Sabah would become completely unsuitable. This is in accordance with the predictions of five of the eight climate/emission scenario combination modelled here, all of which predicted very little change in orangutan distributions in these areas.

The model predictions are relevant to orangutan conservation initiatives as they indicate that under future climates the majority of the range of the orangutan is likely to remain suitable. This indicates that conservation programmes do not need to centre their efforts on particular regions of Borneo and Sumatra that will remain climatically suitable and should instead focus on maintaining genetically viable populations across the range of the orangutan, in areas where human impacts can be more easily controlled. The results also imply that climate change may not necessarily be a major concern for conservation organisations, particularly in comparison to the more pressing anthropogenic threats.

The sensitivity of orangutan distribution patterns to future human population growth, however, is a concern. Large increases in human population densities will lead to an intensification of the many pressures currently facing the orangutan. It seems likely that the threat of hunting will increase, as past human population growth led to increased hunting pressures (Sodhi et al. 2004). Land conversion will occur with increased rapidity, as agricultural land is required to feed the expanding population (FAO 2013). Human population growth was included in the model as an approximate measure of human impacts; however, it must be viewed as a considerable underestimation of the diverse human pressures. In addition, the calculation assumed that human population growth will occur at the same rate across the world, while in reality it is likely that human population growth will be greater in developing countries than in developed countries and in urban areas than in rural areas (Montgomery 2008). However, this was

the best available estimate and can still provide an indication of the effect of human population growth on the orangutan distribution. The model clearly shows that human population density is an important threat to the future distribution of the orangutan and that anthropogenic factors will therefore be critical in determining the future of the species.

The predicted range reductions for the orangutan were similar to those found for chimpanzees, which were predicted to lose 10% of their current range by 2100, but considerably smaller than the 75% reduction predicted for the gorilla (Lehmann et al. 2010a). The African ape model utilised a somewhat bleaker climate scenario, predicting by 2100 temperature increases of 5.2°C, which is more than 1.5 °C warmer than the most extreme scenario modelled here, and precipitation increases of 15% (Lehmann et al. 2010a), which is similar to that predicted under the CSIRO models (A2a=14.33% increase across the range of the orangutan, B2a=12.13% increase across the range of the orangutan). It is possible that the more severe predictions for the gorilla are a consequence of the slightly more pessimistic scenario modelled, as gorillas are particularly restricted by temperature (Lehmann et al. 2010a). Alternatively, it may be that the gorilla is more vulnerable to future climate change than the other great apes; indeed, the size of the difference in predictions suggests that this is likely to be the case. Finally, it is important to emphasise that even the African ape model does not represent the absolute worst case scenario, and so climate change may be considerably more severe than examined here (global mean temperatures may increase by as much as 6.4°C by 2100; Solomon 2007), and as a result may have far more detrimental effects.

3.4.2 Causes of the range reduction under the CSIRO model

One of the major advantages of time budget models over bioclimate envelope models is that they can provide indications of the effects that climate change will have on behaviour. This can highlight the factors that lead to particular regions becoming unsuitable in the future. Although most of the models did not predict a great reduction in the range of the orangutan, this reduction was predicted to be fairly substantial under the CSIRO model. This appears to be the result of an increase in feeding time caused by more fruit in the diet; feeding time and the percentage of fruit in the diet were both higher in the future than in the present in the areas predicted to become unsuitable by 2080. This may be caused by changes in precipitation patterns; the CSIRO model, under both emissions scenarios, predicted the largest increase in precipitation over the current range of the orangutan. Looking back at the equations on which the model is based (Table 2.5), it is clear that the percentage of fruit in the diet has a quadratic relationship with precipitation of the warmest quarter, meaning that after a certain point, increases in precipitation increase the percentage of fruit in the diet. A greater percentage of fruit in the diet in turn increases feeding time. This suggests that these regions are becoming unsuitable as a result of a high percentage of fruit in the diet and hence high feeding time requirements.

A possible explanation for this could be that the increased precipitation will lead to an increase in the availability of fruit, resulting in an increase in fruit consumed. However, there is evidence that an increase in rainfall actually reduces the net primary productivity of tropical forests (Schuur 2003), and also disrupts fruiting patterns (Wright 1996). In Ketambe it was shown that three years with lower than average rainfall were associated with very high fruit production. It was suggested that the lower

fruit production in wetter years may be a result of an increase in fungi under the wetter conditions (van Schaik 1986). At Tanjung Puting, a year in which many trees failed to fruit was also one in which there was heavy and prolonged rainfall (Galdikas 1988). Therefore, it seems likely that fruit availability will actually decrease with increased rainfall.

If this is the case, an alternative explanation for the increased percentage of fruit in the diet is that orangutans have to spend more time feeding on less preferred fruits which have lower nutritional quality and/or greater extraction times, as a result of an overall decrease in fruit availability. It has been shown, for example, that orangutans preferentially select fruit with high pulp mass per swallowed unit of pulp and seed, indicating that they are sensitive to handling time (Leighton 1993). In addition, during periods of low fruit availability, orangutans have been shown to focus more on fruits and seeds such as *Neesia* seeds, which are difficult to extract (Knott 1998). The quadratic relationship suggests that with the initial increases in rainfall, orangutans respond to the lower availability of fruit by focussing more on their fallback foods such as leaves and bark. Once rainfall exceeds a certain point, however, orangutans are no longer able simply to replace their dependence on fruit with leaves or bark. It has been shown that during months in which orangutans are forced to eat large quantities of leaves and bark, they are in severe negative energy and protein balance (Knott 1998, Vogel et al. 2011). Orangutans would therefore be forced to focus more of their feeding time on fruit, including less preferred fruit with lower nutritional quality and/or higher handling times, in order to consume sufficient calories and protein for survival.

Alternatively, it is possible that the predicted relationship between fruit and rainfall is the result of the El Niño Southern Oscillation, which brings drought to South-east Asia, stimulating fruit production (Curran et al. 1999). Theoretically, this could lead to a

relationship between low rainfall and greater fruit consumption. However, the rainfall data on which the relationships are based are averaged over 50 years, while most of the fruit consumption data were also averaged over a number of years; therefore the data in this model represent site averages and not values found during extreme years. Furthermore, although the severity of El Niño events can vary across regions (Slik 2004), it does affect both Borneo and Sumatra (Kinnaird and O'Brien 1998, Kirono et al. 1999, Taylor et al. 1999), so average rainfall values across the islands should all be affected by these weather events. This means that although El Niño may explain inter-annual variability in fruit consumption at an individual site, it should not be a major contributing factor to inter-site variability in average fruit consumption.

Thus, the results of the CSIRO model suggest that some areas may be unsuitable in the future due to prohibitively high feeding time requirements as a result of lower quality fruit associated with higher rainfall. It is important to emphasise that there is considerable uncertainty in climate predictions, and so the results produced under the CSIRO model, and indeed all the models, should be treated with caution. Furthermore, extrapolating the time budget equations beyond the range of climates in which orangutans currently occur may not accurately depict the way that orangutans will in fact respond to these conditions. However, the models do highlight the potential vulnerability of the orangutan to changes in precipitation levels, leading to increases in feeding time. As the climate predictions utilised in this study were by no means a worst case scenario, further increases in rainfall or increasingly frequent periods of extreme rainfall are possible, and these could have devastating effects on the distribution of the orangutan.

3.4.3 Predicted changes to time budget allocations where the orangutan is predicted to survive

Time budget allocations were also investigated in the areas where the orangutans are predicted to be able to survive in the future. These were compared to time budget demands in the same areas but under current conditions, to highlight the changes that can be expected to occur with novel climates. Interestingly, the percentage of fruit in the diet was also predicted to increase in the future in these areas (with five out of eight model/emissions scenario combinations predicting an increase). Four of the five model/emissions scenario combinations that predicted significant increases in the percentage of fruit in the diet were those that predicted the greatest increase in rainfall over the range of the orangutan. This indicates that predicted increases in rainfall may be contributing to the high percentage of fruit in the diet under future conditions in both the areas where the orangutans will continue to survive and those that will be made unsuitable. This is likely to be related to the impact of rainfall on the availability of fruit.

Resting time demands were predicted to decrease in the future, (with six out of eight model/emissions scenario combinations predicting a decrease), although these effects will probably depend heavily on the impact of climate change on forest cover, an effect which could not be included in the model. The predicted reduced time spent resting is likely to be linked to the increased reliance on fruit, as fruit requires less enforced resting time for digestion (Korstjens et al. 2010). Reduced resting time predicted for the orangutan contrasts with the results found for the African apes, which were predicted to experience an increase in resting time under climate change as a result of a shift towards greater folivory; this effect was much more pronounced in chimpanzees than gorillas

(Lehmann et al. 2010a). This difference in predicted resting time may be attributed to the poor quality of forage in South-east Asian rainforests, which prevents the orangutan from shifting towards greater folivory, as this leads to both protein and energy deficiencies (Knott 1998, Vogel et al. 2011).

Moving time demands may become increasingly high in the future (with five out of eight model/emissions scenario combinations predicting an increase). If indeed the availability and quality of fruit decline in the future as suggested above, this may necessitate greater moving time allocations to search for food. In addition, higher moving time demands will in turn lead to increased energy requirements, which will have a knock-on effect on other time budget variables. Feedback loops like this are not currently included in the model, but it is important to consider them as they may lead to exaggerated effects of climate change on orangutan populations.

Feeding time appears less likely than the other time budget variables to change in the future, with only three model/emissions scenario combinations predicting an increase in feeding time demands. This may be related to an increased reliance on lower quality food with higher extraction times, requiring higher feeding time allocations. Thus, the dietary changes that are predicted to occur in the future are likely to lead to changes to orangutan behaviour, forcing them to spend more time feeding and moving but less time resting.

3.4.4 Predicted changes to maximum ecologically tolerable group sizes where the orangutan is predicted to survive

The models did not produce a consistent effect of climate change on maximum ecologically tolerable group sizes. Although under the CSIRO models group sizes were predicted to decrease across the range, the other models predicted either an increase in

group size or no significant change. Group size in orangutans therefore appears to be sensitive to variations in climate predictions, but if indeed a group size of close to one individual is a viable minimum, orangutans appear to be somewhat buffered against the effects of climate change. However, if climate change does follow the pattern predicted by the CSIRO model, orangutans will experience even greater time budgeting stress in the future and a lower degree of social flexibility. This means that orangutans will not only lose a considerable portion of their range, they will also have a reduced ability to respond to any further habitat degradation within their remaining distribution. Considerable increases in precipitation clearly represent a serious threat to the orangutan.

3.5 Conclusion

The results of this study highlight the precarious balance between climate, behaviour and biogeography – if one of the components is affected this can have knock-on effects on other variables, exaggerating the consequences for orangutan populations. Moving and feeding time demands, for example, are predicted to become more severe in the future, while resting time may become less restrictive, and these changes will have secondary effects on other variables. Overall, the results indicate that the current range of the orangutan might decline by approximately 3-7% by 2080 as a direct result of climate change and human population growth. Although this is not a considerable decline, even a range reduction of 5% may have a dramatic effect on the survival of the two orangutan species, particularly as suitable habitat becomes more fragmented through deforestation.

4. The Effects of Network Topology on Potential Disease Transmission: A Comparison between Orangutans and Chimpanzees

4.1 Introduction

4.1.1 The threat of disease to the survival of the great apes

Disease transmission is one of the key threats to the survival of primate species worldwide (Nunn and Altizer 2006). An Ebola epidemic, for example, killed an estimated 5000 gorillas in Lossi National Park alone (Bermejo et al. 2006), while in the Minkebe forest of Gabon, estimated declines of 98% of gorillas and 99% of chimpanzees were suspected to result from an Ebola outbreak (Huijbregts et al. 2003). Infectious diseases are now emerging at an accelerated rate in both human and animal populations (Chapman et al. 2005), while the increased deforestation and forest fragmentation that is expected to occur in the future, combined with the rise of ecotourism, will increase contacts between humans and wildlife and lead to a much

higher risk of inter-specific disease transmission (Chapman et al. 2009). This will be particularly problematic for non-human apes, which share a susceptibility to many of the diseases that infect humans (Woodford et al. 2002). In addition, the slow life histories of the great apes makes them particularly vulnerable to population declines as it takes many years for populations to recover (Ryan and Walsh 2011). In order to be able to plan effective conservation strategies for the orangutan it is therefore extremely important to gain information about the vulnerability of these species to disease. The significance of disease transmission as a threat, and the susceptibility of orangutan populations to epidemics need to be assessed. Insights into potential disease spread can be obtained by using social network analysis to look at contact patterns, which provide the opportunity for infectious disease to spread within a population. This method can be used to assess the vulnerability of orangutans to disease, but for a relative assessment of disease risk it is useful to compare the results with those from a closely related species, the chimpanzee. This will also illustrate the way in which differences in behaviour and social organisation between the two species impact predicted disease risk and hence the potential risk of disease to orangutans living in more social conditions, such as rehabilitation centres.

Awareness of the threat of disease among the great apes has increased considerably in recent years and guidelines relating to both visitor hygiene and behaviour have been outlined and implemented at ecotourism and research sites to prevent disease transmission from humans (Lukasik-Braum and Spelman 2008, Macfie and Williamson 2010). However, these measures are often difficult to enforce, particularly among tourists who have paid considerable fees to visit the apes (Wallis and Lee 1999, Sandbrook and Semple 2006). Consequently, these measures should not be relied upon as the only method of protecting apes from disease (Ryan and Walsh 2011). One of the

other major preventative measures used to reduce the impact of disease is vaccination. Selective vaccination, i.e. vaccinating only those individuals that are likely to play a key role in disease spread, offers the opportunity to have a considerable impact on disease whilst minimising costs as well as the negative effects on the animals from invasive vaccination procedures (Haydon et al. 2006). This process relies, however, on the accurate identification of these key individuals. Social network analysis provides methods through which the central individuals in potential disease spread can be identified and their impact on transmission dynamics assessed, to determine if the targeted vaccination of these animals would be an effective strategy. This method has not yet been applied to disease transmission in orangutans or wild chimpanzees, and doing so will provide important new insights for conservation planning for these species.

4.1.2 The risk of disease spread among orangutans

Orangutans have been observed to be susceptible to a range of infectious diseases (Mackinnon 1974, Collet et al. 1986, Warren et al. 1999, Wolfe et al. 2001, Kilbourn et al. 2003, Reid et al. 2006, Mul et al. 2007); however, the actual spread of these diseases has not previously been investigated in either a field or a modelling study. This is clearly an area in which more information is needed to ensure that the risks are understood and effective prevention strategies are in place.

The rampant deforestation and forest fragmentation that continue to occur across Borneo and Sumatra (Miettinen et al. 2011a) will bring humans and orangutans into ever closer proximity. This will inevitably increase the risks of disease transmission from both humans and their livestock to orangutans (Chapman et al. 2009). Forest fragmentation may also force animals to crowd into remaining fragments, leading to

lower food intake and increases in stress, which will reduce the ability to fight disease (Nunn and Altizer 2006). This may also lead to population reductions and a subsequent loss of genetic diversity, making the species more susceptible to disease (Breed et al. 2009). There is some evidence from primates that fragmentation can lead to increases in disease, possibly by increasing proximity to humans and consequently the risk of inter-specific disease transmission. Red colobus monkeys living in fragmented forests, for example, harbour higher levels of gastro-intestinal parasites than those in unfragmented forests (Gillespie and Chapman 2008). The genetic similarity between the *E.coli* bacteria harboured by the primates around Kibale with those from the humans and livestock in the nearest village increases as the level of forest fragmentation increases (Goldberg et al. 2008b). Finally, hamadryas baboons (*P. hamadryas*) living in closer proximity to humans had a higher prevalence of intestinal parasites than those with less human contact (Ghandour et al. 1995). It is therefore likely that forest fragmentation will have a negative effect on orangutans in terms of disease prevalence, by bringing them into closer proximity to humans and also to each other, thereby increasing both inter- and intra-specific disease transmission.

The rise of ecotourism and the increase in the number of research sites and researchers may also have a negative impact in terms of disease and parasite load (Nizeyi et al. 1999, Graczyk et al. 2001, Graczyk et al. 2002, Nizeyi et al. 2002, Kalema-Zikusoka et al. 2005). At Kibale, gastrointestinal bacteria from chimpanzees have been found to be more similar genetically to those from humans engaged in research and tourism than those from the inhabitants of a local village (Goldberg et al. 2007). Similar results were found for gorillas in Bwindi; genetic similarity between *E.coli* bacteria in gorilla and human faeces was highest for the tourism group which had high human contact, intermediate for the research group with intermediate human contact and lowest for the

wild group with very little human contact (Rwego et al. 2008). This is also one of the few cases for which there is direct evidence of a negative effect on orangutans. Orangutans at Bukit Lawang, a site with high contact with tourists, were found to harbour a higher richness of metazoans and a higher prevalence of parasites than at Ketambe where human presence is lower (Foitová et al. 2009). Thus, ecotourism and research may pose serious threats to the orangutan in terms of their impact on disease.

There is evidence that rehabilitant orangutans may suffer from increased disease prevalence (Wolfe et al. 2002, Kilbourn et al. 2003). This is important for two reasons. Firstly, as deforestation and hunting continue there will be a constant stream of orphans entering orangutan rehabilitation centres (Russon 2009). Although new regulations state that these orphans can only be released into areas with no wild orangutans, there is still a risk that disease will be transmitted to migrating individuals (Foitová et al. 2009). Secondly, these studies suggest that the reason for the increase in disease is the higher densities at which the rehabilitants live (Wolfe et al. 2002). If this is the case, it does not bode well for a future in which orangutans are likely to be forced to live at ever higher densities in the few fragments of forest that remain to them. Finally, in the future it is likely that reintroduced orangutans will comprise a large proportion of the overall population of orangutans. Protecting these orangutans from disease may be essential for the long-term survival of the species.

4.1.3 The effect of sociality on disease risk: a comparison with chimpanzees

There is some evidence to indicate that orangutans may be less susceptible to disease than the other great apes as a result of their relatively asocial nature. Orangutans are rarely observed to groom one another, a behaviour commonly employed to remove ectoparasites, indicating that perhaps disease (at least that related to ectoparasites) is

less of a problem to these species (Nunn and Altizer 2006, Knott and Kahlenberg 2007). It has been suggested that the lower mortality observed in orangutans compared to the African apes may be a result of their lower levels of gregariousness, leading to less disease spread (Wich et al. 2004). One study of gastrointestinal parasites found that the total number of species found was less in orangutans than chimpanzees and gorillas, which again may be related to species differences in social organisation (Mul et al. 2007). Thus, it seems likely that the lower gregariousness of the orangutan leads to a lesser susceptibility to disease than that experienced by the more gregarious African apes. In this chapter, this will be examined by comparing the predicted vulnerability of the orangutans with that of chimpanzees. This will highlight the way in which differences in social structure impact predicted disease dynamics, and will provide insights into the relative level of threat that disease poses to the orangutan, compared to a closely related species. The chimpanzee results will also provide an indication of the risk of disease to orangutans forced into more social situations, such as those in rehabilitation centres, where orangutans congregate in large groups at feeding platforms and then disperse again into the forest (Russon and Galdikas 1993, Russon et al. 2007, Kuze et al. 2008, Russon 2009), leading to a more gregarious form of fission-fusion behaviour than observed in the wild. Finally, chimpanzees are also threatened by the intensification of disease pressures described above, caused by the increase in deforestation and the rise of ecotourism, and so the analysis of a chimpanzee network will also improve current understanding of the level of this threat to the future survival of the chimpanzee.

4.1.4 Investigating disease transmission using social network analysis

Studying the transmission of disease through populations of wild, endangered species in the field can be difficult, as studies are often restricted by the sporadic nature of epidemics. Recent developments in social network analysis, however, have produced a number of methods that can be used to investigate a range of disease related questions for any population for which association data are available (Croft et al. 2008). These methods, by virtue of using computer models, do not suffer from many of the ethical issues that can occur in experimental studies of disease transmission in wild populations. This is particularly useful for endangered species such as the orangutan and the chimpanzee, for which it would be extremely difficult to justify experimental studies such as introducing disease into a group to investigate disease spread or experimentally removing individuals to explore the effect on network fragmentation.

It is important to note that the social network analyses used here relate only to infectious diseases spread by close association or physical contact, such as the respiratory diseases which are known to pose a considerable threat to great apes (Wallis and Lee 1999). In addition, the analyses are only relevant to diseases to which the animals have not previously gained immunity, and consider only within-species disease transmission, while in reality disease often spreads between species including to and from humans (Kaur et al. 2008, Köndgen et al. 2008). Social network analysis uses association data to create social networks representing the relationships within a social group or population. Individuals are represented by nodes and if two individuals have been observed to associate, their respective nodes are connected by an edge (Croft et al. 2008). Networks can be either binary or weighted; in binary networks relationships are either present or absent while in weighted networks the strength of relationships is also

included (Whitehead 2008). Figure 4.1a is an example of a binary social network for five individuals, represented by the blue squares. The lines connecting the squares (edges) indicate a relationship between the two individuals. Figure 4.1b is an example of a weighted network, where the thickness of the edges indicates the strength of the relationship.

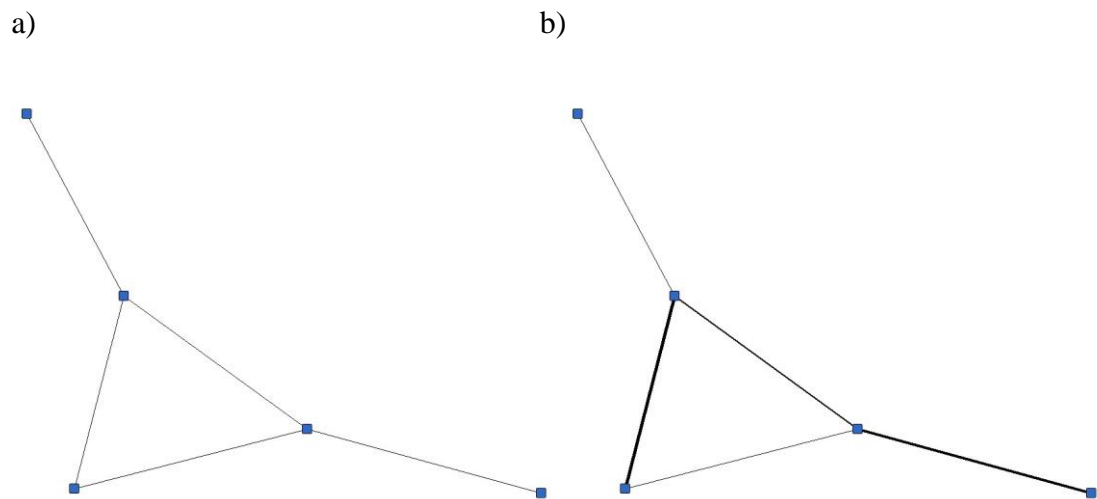


Figure 4.1: a) An example binary social network and b) an example weighted social network

Social network analysis provides a means of exploring the structure of social groups and measuring particular properties of both the overall network and the individuals within it that may be important for the spread of disease. The values of certain network properties can be used to predict how rapidly and how completely a disease could spread in a network (Watts and Strogatz 1998, Wey et al. 2008). Properties of individuals within the network can also be investigated, to identify animals that may be more susceptible to infection or more influential in spreading disease (Corner et al. 2003). Simulations can be performed in which individuals are removed from the network and the extent of network fragmentation measured (Lusseau 2003). This

indicates not only the impact of the death of individuals on the network, but perhaps more importantly the effect that potential vaccinations have on disease spread by disrupting disease pathways (Newman 2003b). These analyses can produce an overall indication of the vulnerability of a population to disease.

4.1.5 Network properties and their implications for disease transmission

There are a number of particular network properties that are associated with more complete or more rapid disease spread and that can be measured using social network analysis. One property that is commonly measured to estimate the speed with which disease may spread is the distribution of individuals' degrees; the degree of an individual is the number of its direct contacts (Freeman 1978). It has recently been observed that a lot of large networks have a degree distribution that is better described by a power law distribution than the Poisson distribution that is found in random networks (Croft et al. 2008). Networks with power-law degree distributions have been termed scale-free networks (Wang and Chen 2003). Networks with scale-free degree distributions are characterised by the presence of a number of individuals with extremely high degree relative to other members of the group (Keeling and Eames 2005). This property is important as epidemics are predicted to spread extremely quickly in scale-free networks, as once the individuals with very high degree become infected, the disease can rapidly spread to a large number of group members (Barthelemy et al. 2004). A number of studies on animal social networks have looked for scale-free degree distributions (Lusseau 2003, Manno 2008, Kanngiesser et al. 2011); however, it has been argued that most animal networks in fact contain far fewer individuals (usually only a few tens or hundreds of nodes) than would be necessary to test robustly for this property (James et al. 2009). As both the orangutan and

chimpanzee networks explored in this study are also small (only 37 and 55 individuals respectively; see below), this test will not be performed here. There are a number of other network properties of relevance for disease transmission that can be reliably measured for small networks, including the number of isolated clusters, the density, the diameter, the clustering coefficient and path length of the network and the presence of positive assortativity by degree.

The number of isolated clusters in a population is important as if all of the individuals in a network are connected in one component, disease can clearly spread to all members. However, if the network is separated into a number of components that are not connected, then disease will become isolated in the component in which it arises (Sundaresan et al. 2007, Griffin and Nunn 2012).

The density of the network simply represents the number of connections present in relation to the total number of possible connections, with higher densities associated with more rapid and complete disease spread (Wey et al. 2008). The diameter is the maximum shortest distance between two nodes in the network; a low diameter indicates that the group is cohesive and that disease could spread rapidly between individuals (Sueur et al. 2011). High clustering coefficients and low path length are associated with ‘small-world networks’, networks in which any two individuals can be connected by only a small number of links (Milgram 1967, Watts 1999). Diseases are predicted to spread relatively easily through small-world networks (Watts and Strogatz 1998). The clustering coefficient indicates the degree to which an individual’s immediate neighbours are connected (Krause et al. 2007), while average path length is the mean of the shortest paths connecting any two individuals in the network (Croft et al. 2005). Low path length suggests very rapid disease spread as all individuals can be connected through a small number of associates (Watts and Strogatz 1998, Sundaresan et al.

2007). A high clustering coefficient implies that network members are very cliquey, in that a lot of an individual's associates are also associated with one another. This means that disease can quickly spread to a high proportion of cluster members (Sundaresan et al. 2007). However, high clustering alone does not always encourage disease transmission as at very high levels of clustering diseases may become isolated and fail to spread between clusters (Newman 2003a, Newman and Park 2003, Croft et al. 2004). In small world networks, where high clustering is accompanied by low path length, the short paths connect clusters such that disease spreads rapidly (Keeling and Eames 2005, Eames 2008). Small-world properties have been found in a number of animal societies to date, including bottlenose dolphins (*Tursiops truncatus*; Lusseau et al. 2006), chimpanzees (Kanngiesser et al. 2011), killer whales (*Orcinus orca*; Guimarães et al. 2007), possums (*Trichosurus vulpecula*; Porphyre et al. 2008), manakins (*Pipra filicauda*; Ryder et al. 2008), rhesus macaques (*M. mulatta*; Brent 2009) and guppies (*Poecilia reticulata*; Croft et al. 2004).

In networks that express positive assortativity by degree, diseases would be expected to spread extremely quickly (Krause et al. 2007). Positive assortativity by degree means that individuals in the network with lots of contacts are connected to a lot of other group members who also have lots of contacts, i.e. highly connected individuals preferentially associate with other highly connected individuals. As a consequence of having a lot of contacts, these highly connected individuals are both more likely to become infected and once infected will rapidly spread the disease by passing it on to their highly connected associates (Croft et al. 2005). Diseases, however, may be confined within the cliques of highly connected individuals and not spread to more peripheral sections of the network (Newman 2003a). Positive assortativity by degree is a common feature of

human social networks (Newman 2002) and has also been observed in bottlenose dolphins (Lusseau and Newman 2004) and guppies (Croft et al. 2005).

Thus, there are a range of social network properties that can provide useful information about both the likely speed and extent of disease transmission. Measuring these properties should provide important information about how the structure of the orangutan and chimpanzee networks and their different patterns of association impact upon the risk of disease transmission in these species.

4.1.6 Individual properties and their implications for disease transmission: highly central superspreaders

In addition to overall network properties, those associated with particular individuals can have implications for disease spread. The position of individuals within a social network can be very important for both the probability of acquiring infection and the ability to spread infection within the group (Krause et al. 2007). Importantly, this is one area of social network analysis where predictions have been compared against observed patterns of disease transmission (Corner et al. 2003, Godfrey et al. 2009, Drewe 2010). The predictions generated by network analysis have been shown to be largely accurate when compared against actual infection rates in animal populations, providing support for the ability of metrics associated with individuals to accurately represent disease risk. As described above, for example, individuals who have a lot of contacts (described as having a high degree), are predicted to have a high chance of acquiring infection. This is supported by evidence from possums in which individuals that became infected with tuberculosis were shown to be those that had the highest degree (Corner et al. 2003). A higher degree in a crevice sharing network was associated with a greater tick load in gidgee skinks (*Egernia stokesii*; Godfrey et al. 2009), while high degree in networks of

grooming given and aggression received was associated with becoming infected with tuberculosis in meerkats (*Suricata suricatta*; Drewe 2010). Other measures of centrality can also be associated with higher infection risks; for example, high closeness centrality (the sum of the distance to all other individuals in the network) and betweenness centrality (the number of shortest paths between individuals on which the animal lies) have been associated with increased risk of infection with tuberculosis in possums (Corner et al. 2003). High betweenness in a meerkat aggression network was also associated with higher probability of tuberculosis infection (Drewe 2010). Finally, high eigenvector centrality can be related to high vulnerability to infection (Bell et al. 1999). Eigenvector centrality takes into account the associations of network neighbours so an individual with higher eigenvector centrality is connected to lots of other individuals who also have a lot of connections (Bonacich 1972).

Individuals with high centrality are also able to spread disease to a large proportion of group members. These individuals are often described as ‘superspreaders’ and have been found to be a normal feature of disease spread in humans (Lloyd-Smith et al. 2005). Indeed, it has been shown that for a range of diseases around 20% of the host population are responsible for at least 80% of disease transmission (Woolhouse et al. 1997). Similarly, in many animal populations, such as those of deer mice (*Peromyscus maniculatus*), around 20% of the population are responsible for about 80% of the contacts, which may be indicative of a superspreader role (Clay et al. 2009). A simple measure of node degree is a good indication of the importance of the individual in the network and also the ability to spread disease. As mentioned previously, scale-free networks are characterised by individuals with very high degree; however, testing for a scale-free degree distribution on the ape networks would not be appropriate given the small number of individuals involved. Despite this, it is still interesting to explore

variation in individual degree or any skew in the degree distribution as this could have implications for disease spread (Croft et al. 2008, James et al. 2009).

There are a number of other measures of centrality that may also be important in disease spread. For diseases with low virulence the strength of a relationship may be more important as these diseases will require repeated contacts before infection (Wey et al. 2008). The strength of relationships in an Australian sleepy lizard (*Tiliqua rugosa*) network of refuge use, for example, was an important correlate of tick load (Leu et al. 2010). Closeness centrality is another measure of superspreader ability, as this indicates the potential to spread disease to the entire network and not just direct contacts (Wey et al. 2008). In addition, ‘brokers’ or individuals that connect groups that would otherwise be isolated, could be very important for spreading disease between components in a network (Lusseau and Newman 2004, Ortiz-Pelaez et al. 2006, Wey et al. 2008). In network terminology, ‘brokers’ are defined as individuals with high betweenness, which is measured as the number of shortest paths on which the individual lies (Lusseau 2007). Individuals with high betweenness may be important in spreading disease; for example, it was shown that the movement of badgers (*Meles meles*) between groups may be causing much of the spread of tuberculosis (Vicente et al. 2007). In territorial animal populations it has been suggested that transient individuals that travel between areas could act as superspreaders by linking groups in this way (Cross et al. 2009, Craft et al. 2011). Individuals with high eigenvector centrality may also be important in spreading disease (Bell et al. 1999). Thus, there are a number of characteristics that could make individuals not only more susceptible to disease, but also more effective at spreading infection within the group.

In addition to variation between individuals, there may be differences between the sexes in these metrics, implying that males and females differ in their importance in disease

transmission. Female orangutans appear to be the more gregarious sex, particularly sexually-active females (van Schaik 1999, Mitra Setia et al. 2009), and so it is possible that they will have higher values on average than males for some social network metrics. In contrast, males are generally found to be the more social sex among chimpanzees (Wrangham 2000). This could have implications for the importance of the different sexes in disease spread. Thus, it is also important to test for differences in individual measures between the sexes as this could demonstrate if males and females (and for orangutans, unflanged males, flanged males and females) differ in both their susceptibility to disease as well as their role in disease spread.

The identification of superspreaders is important for conservation measures aimed at preventing epidemics as these individuals could be targeted in vaccination programmes. Vaccination is generally used when a population is a reservoir for a disease threatening humans or livestock, or to protect endangered species from epidemics (Plumb et al. 2007). This strategy has achieved varying levels of success in different populations and against different diseases (Blancou et al. 2009). For example, a vaccination programme of African wild dogs (*Lycaon pictus*) in the Serengeti against rabies failed when the wild dogs became extinct in the area, probably a result of an ineffective vaccine although the possibility remains that extinction was caused by another disease such as canine distemper virus (Gascoyne et al. 1993, Woodroffe 2001). There have also been a number of successes; for example, red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*) and coyote (*Canis latrans*) rabies vaccination programmes have been relatively successful so far in North America and Europe (Brochier et al. 1996) and gorillas were successfully vaccinated against measles (Hutchins et al. 1991). The vaccination of wild animals has disadvantages though, as it is extremely expensive and difficult to implement, as well as being invasive for the animals in question. Live vaccines may

induce disease in the intended or even unintended hosts (Blancou et al. 2009), while handling and restraining animals can cause stress, which may lower their immune response (Cabezas et al. 2006). Vaccinations may lead to the selection and spread of non-vaccinal strains of the disease or reduce the selection pressure for natural resistance to diseases - although this is less likely to be a problem for highly virulent diseases for which there is usually limited natural immunity (Blancou et al. 2009). Most of the disadvantages associated with vaccinations could potentially be reduced if vaccinations were targeted at a few key individuals or sexes, enough to achieve herd immunity and thus prevent a widespread epidemic (Craft and Caillaud 2011). This could reduce costs and effort as well as involving fewer animals in the invasive procedures. This technique has not yet been widely applied; however there is some evidence indicating that vaccinating wolf packs that ranged within or near a corridor connecting two subpopulations reduced the overall extent of a rabies epidemic in Ethiopian wolves (*C. simensis*; Haydon et al. 2006). It is possible that targeted vaccinations could provide a useful method of disease prevention for orangutans or chimpanzees in the future. The identification of superspreaders in the ape networks as potential targets could provide valuable information for conservation actions aiming to prevent large scale disease outbreaks.

4.1.7 Assessing the utility of vaccinations on reducing disease spread: the simulation of random and targeted removals

Once superspreaders have been identified, it is useful to assess the efficacy of targeting these individuals in vaccination campaigns. Simulated removals provide a way of examining the effect of individual vaccination on network structure. If the removal of a particular animal destroys many paths connecting different components or individuals

in the network, vaccinating the individual may prevent disease from being transmitted along these paths (Newman 2003b). Individuals can be removed either randomly or in a targeted manner and the effects on network cohesion compared. This will provide an assessment of the potential efficacy of each method in reducing disease pathways and consequently potential disease spread. The removal of an individual from a network can also be interpreted as simulating the death of that individual, as both they and their relationships disappear from the network. Removal simulations can therefore also be used to investigate the vulnerability of the network to member death, in terms of the extent to which it will fragment following the deaths of random or particularly central individuals (Lusseau 2003).

This method has provided a range of results in the networks in which it has been implemented to date. Scale-free networks such as the Internet have been shown to be highly robust to the removal of random nodes, but extremely susceptible to the targeted removal of the most connected nodes (Albert et al. 2000). Networks of Columbian ground squirrels (*Spermophilus columbianus*; Manno 2008), captive chimpanzees (Kanngiesser et al. 2011), dolphins (Lusseau 2003, Lusseau and Newman 2004) and female grooming networks across 11 primate species (Lehmann et al. 2010b) became less cohesive in simulations following targeted removal of individuals with high centrality than following random removals. Pigtailed macaque (*M. nemestrina*) networks became less integrated with the simulated removal of three dominant animals, and in fact following the experimental removal of these animals the frequency of aggression in the group increased (Flack et al. 2006). A killer whale network was more likely to fragment into isolated groups following targeted removals mimicking historic live-captures than after random removals (Williams and Lusseau 2006). Thus, many networks appear to be susceptible to the loss of targeted members. However, this is not

true for all networks studied to date. Although targeted removals caused considerable fragmentation in one colony of leaf-roosting bats (*Myotis tricolor*), the networks of two other colonies studied were resilient to the removal of up to 50% of individuals with both highest degree and betweenness (Chaverri 2010).

Comparing the level of network fragmentation that occurs following targeted and random removals will provide valuable information for conservation regarding the relative value of each method in preventing the spread of disease. If targeted vaccinations emerge as an effective potential strategy, the analyses will identify the individuals that are particularly important in the ape networks and would therefore be good first targets for vaccination programmes.

4.1.8 Chapter aims

1. To provide an indication of vulnerability to infectious disease by examining properties of both binary and weighted orangutan and chimpanzee association networks, including the mean degree and strength, density, diameter, clustering coefficient, path length, the presence of positive assortativity by degree and the number of isolated components in the networks.
2. To identify highly central individuals that are predicted to be both more likely to become infected and more likely to spread disease in the two ape populations. This will be achieved by investigating properties of individuals in the networks (degree, betweenness centrality, closeness centrality, eigenvector centrality, strength, weighted betweenness centrality, weighted closeness centrality and weighted eigenvector centrality).

3. To determine whether one age/sex class is more prone to infection, or more important in transmitting disease, than the others by comparing mean centrality values between different age/sex classes within species.
4. To explore the potential effect of vaccination on disease pathways as well as how vulnerable orangutans and chimpanzees are to the death of group members from disease by simulating random and targeted removals.

4.2 Methods

4.2.1 Orangutan study site

Orangutan (*P.p. wurmbii*) data were supplied and are owned by Dr. Helen Morrogh-Bernard, from OuTrop. These data were collected as part of the OuTrop multi-disciplinary research project in collaboration with CIMTROP, in the Sabangau Forest, Central Kalimantan, Indonesia. The field site is located in the Natural Laboratory for the Study of Peat Swamp Forests (NLSPSF), a 500km² area of protected forest in which development is not permitted (Harrison 2009). It is an area of largely continuous peat swamp forest and supports the largest contiguous orangutan population remaining in Borneo (Morrogh-Bernard et al. 2003). The base camp is situated at Setia Alam (2°19'S 114°00'E) and is located next to a grid of 9km² of mixed-swamp forest in which data collection took place (Morrogh-Bernard 2009). The first orangutan studies began at this site in 1995 and research continues today (Harrison 2009, OuTrop 2013). Tourists are not currently allowed to visit the orangutans.

The mixed swamp forest has a density of around 2.42 orangutans per km² and a total population size estimated to be between 5671-8951 individuals in 1995-1996 (Morrogh-Bernard et al. 2003). The forest has a low density of mast-fruiting trees and so it does

not experience the supra-annual masts characteristic of much of the South-east Asian rainforest, but instead has relatively constant fruit availability throughout the year (Harrison et al. 2010). The site experiences relatively high temperatures and high rainfall all year round, with rain falling in every single month of the year (Harrison 2009). Illegal logging has been a major problem in the Sabangau region in the past. This is particularly problematic for peat swamp forests, as canals are created in order to remove logs, and this process lowers the water table increasing susceptibility to forest fires (Husson et al. 2007). A patrol team was formed in 2003 and this has been relatively successful in eliminating illegal logging and damming the canals within the NLSPSF (Husson et al. 2007). However, illegal logging almost certainly continues to occur in the other parts of the forest (Harrison 2009), which may potentially have implications for disease transmission from humans in the future.

4.2.2 Orangutan association data

Orangutan association data were collected at Sabangau from 2003-2011. Once a focal animal was located it would be followed for as long as 10 consecutive days or until lost. Association data (i.e. presence in the same party) were recorded for the focal individual using instantaneous sampling every five minutes. A party was defined as two or more independent individuals within 50 metres of each other. Mothers with infants were classed as one unit (Morrogh-Bernard 2009). Infants at Ketambe in Sumatra were defined as independent from their mothers when they reached eight years of age as orangutans of eight years and older tend to travel independently of their mother (van Adrichem et al. 2006). However, this age has been shown to vary at different sites and even between individuals; for example, infants often become independent at a younger age if their mother gives birth to another infant (van Noordwijk et al. 2009). All of the

individuals in the orangutan population were clearly independent, except Indy. Indy was six years old at the beginning of the study period, and her mother Indah had given birth to another infant, so Indy could by some measures be considered independent (Harrison 2009). However, Indy spent almost 100% of observation time with Indah until she reached eight years old, and so here Indy is considered socially independent at eight, and only data after this point were included in the analyses.

Focal data were available for 46 orangutans (Appendix A). In total, 165 717 focal scans were recorded. The amount of time each individual was observed over the nine years varied from 65 minutes to over 2500 hours; hence observation time was relatively skewed. Most social analysis hypothesis tests work on the assumption that the data are a random sample of the behaviour of the individuals, and not that the individuals are a random sample of the population. Therefore, sampling individuals as they are encountered, even if this results in skewed observation times, is usually acceptable (Whitehead 2008). In addition, most of the analyses in this chapter were performed on both a binary and a weighted network. Weighted networks were based on association indices (which measure relationships relative to total observation time), which should minimise the effect of any bias in observation effort (Whitehead 2008).

4.2.3 Chimpanzee study site

Chimpanzee (*P.t. schweinfurthii*) data were obtained for the Sonso community in the Budongo Forest Reserve of Western Uganda (1°44'N, 31°33'E). These data were provided and are owned by Professor Klaus Zuberbühler. The Budongo Forest Reserve is an area of approximately 793km² of grassland and forest, with a long history of selective logging (Plumptre and Reynolds 1994). Semi-deciduous tropical rainforest comprises 428km² of the reserve, which contains between 600-700 chimpanzees

(Plumptre and Reynolds 1994, Reynolds 2005). The region experiences relatively high temperatures and rainfall, with a dry season from December to February (Newton-Fisher 1997). Measures to prevent disease transmission between humans and the chimpanzees of Budongo have been implemented. Visitors with symptoms indicating infection are not allowed to enter the forest, and all staff and visitors are required to remain at least seven metres from the chimpanzees at all times. Tourists are not currently allowed to visit the apes. Since 1990 one respiratory epidemic has occurred in the Sonso community, but this was not fatal to the chimpanzees (Reynolds 2005).

4.2.4 Chimpanzee association data

Association data were obtained on the Sonso community (Appendix B). The Sonso community have been studied since 1990 (Newton-Fisher 1997), and live at a relatively high population density of 6.8 chimpanzees per km² (Newton-Fisher 2003). The data were collected between August 2007 and July 2010. A focal animal was followed and party composition recorded in scan samples every 15 minutes. A party was defined as all individuals within 50 metres of the focal animals. Over the three year period, data were available for 55 independent chimpanzees. In total, 34,143 focal scans were recorded. Total observation time for the chimpanzees ranged from a minimum of just over 20 hours to a maximum of nearly 3,097 hours. Chimpanzee infants were defined as independent when they reached five years of age (Reynolds 2005).

4.2.5 Network construction

Where possible, analyses were performed on both a binary and a weighted network. Binary networks are those in which all relationships (edges) are given a value of one while dyads never observed to associate are given a value of zero. In contrast, weighted

networks are those in which all edges are allocated a value based on the strength of the relationship between individuals, i.e. the number of times that they were observed together (Croft et al. 2008). Here, the binary and weighted networks were composed of the same individuals; the only difference was that in the binary networks all edges were given a value of one while in the weighted networks edge values represented association indices. Both networks were analysed in order to determine if the different methods of constructing a network would produce different results. In addition, previous studies of simulated removals have all been performed on binary networks, therefore in order to compare the results from the ape networks with these previous studies it is useful to analyse a binary network. However, weighted networks provide many advantages over binary networks in terms of their ability to represent social systems accurately and so weighted networks were also analysed. Binary networks have been criticised as they require a huge amount of data (usually much more than are available) in order for edges to be reliably designated as absent, while all of the variation in the strength of the edges that are present is lost, as all are allocated the same value of one (Whitehead 2008, Croft et al. 2011). Binary networks can lead to incorrect interpretations of the overall social structure and the position of individuals in the network (Lusseau et al. 2008). In contrast, weighted networks include the variation in the strength of different relationships and hence produce a more accurate representation of the society. When weighted networks use association indices this also controls for biases in observation time.

Another major problem with binary networks is that they usually involve a high level of filtering, particularly of network edges, and this level of filtration is often determined arbitrarily (Lusseau et al. 2008). Filtering is the process of removing individuals or edges from the network that do not meet some predetermined threshold, for example,

removing individuals seen less than a set number of times or those that did not survive for the entire study period, or removing edges between dyads observed associating below a set number of times (Croft et al. 2005). Node filtering is usually employed for both binary and weighted networks and prevents individuals who were rarely observed from biasing the results. For the orangutan network, individuals were removed from further analysis if they were never seen to associate with any other individuals. This was important as the calculation of some of the network measures requires a single connected component (Wasserman and Faust 1994). Furthermore, for the removal simulations, the purpose was to determine the effect of vaccinations on the disease pathways between individuals. As isolated individuals are not involved in any disease pathways, it was not necessary to include them in these analyses. Thus, nine isolated orangutans were excluded from the network. All of the other orangutans were deemed to have been observed for a sufficient amount of time to be included in the network (the minimum number of scans was 13). Individuals were not required to be present in the area for the full nine year study period. The orangutan social system includes many transient individuals who would be excluded from the analysis if this condition were enforced, which would lead to an inaccurate view of the overall orangutan population. All individuals in the chimpanzee network were connected and were therefore included in the analyses. Although some of the chimpanzees may not have been present for the whole study period (some emigrated or died), individuals were observed for a minimum of 20 hours (higher than the minimum for the orangutan), and so all individuals were included in the network to keep the methods consistent with those for the orangutan network.

Filtering of edges is a far more contentious subject. One purpose of filtering edges is to reduce the impact of any errors that may have occurred during data collection, such as

occasionally misidentifying an individual (James et al. 2009). Evidently in a binary network, where all edges are given the same value, such a mistake could have a considerable impact on the structure of the network; thus weak relationships are filtered out to prevent errors from affecting the network (Croft et al. 2008). However, there is no set rule for determining a level of filtration, making this decision difficult and often arbitrary (Croft et al. 2005). In a weighted network the effect of these errors on the results will be considerably reduced and there is consequently less need to filter the network, though even in a weighted network it is often advisable to filter out single interactions which may represent purely chance occurrences (Croft et al. 2005). This may not be necessary for the study of disease however, in which even chance occurrences provide an opportunity for disease transmission (Croft et al. 2008). Since this study focuses entirely on disease, edge filtering was not employed. Although this may lead to the inclusion of incorrect data based, for example, on misidentification, as long as this is a fairly infrequent occurrence this is only a major problem for binary networks, and as all analyses were repeated on a weighted network, this is not a serious concern.

4.2.6 Association indices

In order to construct the weighted network, dyadic association indices were calculated. Dyadic association indices provide a measure of the amount of time that dyads spend in association in relation to the time that they spend apart. These indices standardise the time observed in association by observation effort (Whitehead 2008). The index used here is the Simple Ratio Index.

$$\text{SRI} = \text{AB}/(\text{A} + \text{B} - \text{AB})$$

Where A is the total number of scans in which A was observed, either alone or with other independent individuals, B is the total number of scans in which B was observed and AB is the total number of scans in which A and B were observed together (Cairns and Schwager 1987). Association indices range from zero to one, zero indicating that two individuals were never observed together and one indicating that they were always observed together (Guimarães et al. 2007). These association indices were used to create weighted networks in which an edge between individuals A and B for example was assigned the association index for this dyad.

4.2.7 Calculation of network properties

Seven measures were calculated for the overall binary networks; the number of isolated clusters, the mean degree, density, diameter, clustering coefficient, mean shortest path length and assortativity coefficient. These properties are defined in Table 4.1. Four overall measures were calculated for the weighted networks; mean strength, weighted clustering coefficient, mean weighted shortest path length and the weighted assortativity coefficient. These measures are defined in Table 4.2. The minimum method of calculating the weighted clustering coefficient was employed, as this method is the most useful when analysing flow, for example of disease, between nodes (Opsahl and Panzarasa 2009; see Table 4.2 for definition). A high clustering coefficient combined with a low shortest path length is indicative of a small-world network, and so the networks were classed as either small-world or not dependent on the values of these measures. Binary network measures were calculated using *igraph* (Csardi and Nepusz 2006) while weighted network measures were calculated using *tnet* (Opsahl 2009) in R (R Development Core Team 2011).

Table 4.1: Definitions of binary network metrics (¹Croft et al. 2008, ²Lusseau and Newman 2004)

Binary network metric	Definition
Number of isolated clusters ¹	This is the total number of isolated components in the overall network (before isolates were removed for the later analyses).
Mean degree ¹	<p>The mean degree is the average number of edges that individuals have in the network:</p> $k = \frac{1}{n} \sum_i k_i$ <p>where k_i is the degree of node i.</p>
Density ¹	<p>The density is the number of edges present in the network compared to the total possible number of edges that could be present:</p> $\Delta = \frac{2E}{n(n-1)}$ <p>where E is the total number of edges in the network and n is the number of nodes. The density ranges between 0 (no edges) to 1 (all possible edges are present).</p>
Diameter ¹	The diameter is the length of the maximum shortest path between two nodes in the network.
Mean clustering coefficient ¹	<p>The clustering coefficient is the average proportion of a node's contacts that are also connected to each other. The clustering coefficient ranges from 0 to 1, with values approaching 1 indicating that most individuals' neighbours are also connected to each other.</p> $C = \frac{1}{n} \sum_{i=1}^n \frac{2t_i}{k_i(k_i-1)}$ <p>where t_i is the number of triangles of which node i is a part. A triangle is where three nodes are all connected to each other, forming a triangle in the network.</p>
Mean shortest path length ¹	<p>The mean shortest path length is the average of all the shortest paths connecting all dyads in the network.</p> $L = \frac{1}{\frac{1}{2}n(n-1)} \sum_{i < j} d_{ij}$ <p>where d_{ij} is the mean shortest path between nodes i and j.</p>
Assortativity coefficient by degree ²	The assortativity coefficient by degree is the Pearson correlation coefficient between the degrees of adjacent nodes in the network. This measures the extent to which individuals in the network preferentially assort by

	degree. This ranges from -1 indicating maximum negative assortativity to 1, indicating maximum positive assortativity.
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Table 4.2: Definitions of weighted network metrics (¹Croft et al. 2008, ²Opsahl and Panzarasa 2009, ³Newman 2001, ⁴Kerth et al. 2011)

Weighted network metric	Definition
Mean strength ¹	<p>Mean strength is the average weight of the edges in the network.</p> $s = \frac{1}{n} \sum_i s_i$ <p>where s_i is the strength of node i.</p>
Mean weighted clustering coefficient ²	<p>The minimum method of calculating the mean weighted clustering coefficient was employed. This method allocates a value to each triplet based on the value of the weakest edge within the triplet. A triplet here refers to three nodes connected by two edges (an open triplet), or three edges (a closed triplet). Once triplet values are defined, the value of closed triplets is divided by the value of all triplets:</p> $C_\omega = \frac{\sum \tau \Delta \omega}{\sum \tau \omega}$ <p>where $\tau \Delta \omega$ represents the total value of closed triplets and $\tau \omega$ the total value of all triplets. This measure ranges from 0 to 1 with values approaching 1 indicating that most of an individual's close contacts also have strong relationships with each other.</p>
Mean weighted shortest path length ³	<p>The mean weighted shortest path length is the average of the shortest paths in the network, including the weights of edges in the calculation. Strong paths are given a low cost and weak paths a high cost (by inverting associating indices) and the mean shortest path defined as the path that involves the least total cost. This is calculated using Dijkstra's algorithm. This value is normalised by dividing by the inverse of the mean edge weight in the network. Each unit therefore represents one step of average edge weight in the network.</p>
Weighted assortativity coefficient by strength ⁴	<p>The assortativity coefficient by strength is the Pearson correlation coefficient between the strength of adjacent nodes in the network. This measures the extent to which individuals in the network preferentially assort by strength. This ranges from -1 indicating perfect negative assortativity to 1, indicating perfect positive assortativity.</p>

For both the binary and the weighted networks, values for the clustering coefficient, mean shortest path length and assortativity coefficient were then compared with the distribution of these values from 10,000 randomisations of the network. This determines if the result is significantly different from chance or simply the result of the number of edges, nodes and weights in the network (Sundaresan et al. 2007). Randomisations are necessary for testing hypotheses on social networks as the data are dependent and therefore violate the assumptions of most standard statistical tests (Whitehead 2008). Randomisations were performed using the link reshuffling method in the tnet package (Opsahl 2009) for R (R Development Core Team 2011). This method randomly rewires links and their associated weights between group members. This introduces a high level of randomisation as it reshuffles both weights and the network topology while preserving the degree distribution (Opsahl et al. 2008). It is important to preserve the degree distribution to control for differences in levels of gregariousness (Whitehead 2008). The degree distribution can also have a strong effect on network measures, so simply comparing values to those from Erdos-Renyi random graphs (which have a Poisson degree distribution, rarely observed in nature) is a poor test of significance (Opsahl et al. 2008, James et al. 2009). For the binary networks, all weights are equal to one; therefore this method simply rewires the connections. Ten thousand randomisations were permuted and the value from the orangutan/chimpanzee network defined as significantly different from random if it was within the lowest 2.5% or highest 2.5% of the distribution of random values.

4.2.8 Calculation of individual properties

The investigation of the potential impact of different individuals in spreading disease required the calculation of a number of individual network properties. These metrics

estimate how central each individual is in the network. Four measures were calculated for the binary network, and their weighted counterparts calculated for the weighted network. The binary measures were the degree centrality, closeness centrality, betweenness centrality and eigenvector centrality (Table 4.3) and the weighted measures were the strength, weighted closeness centrality, weighted betweenness centrality and weighted eigenvector centrality (Table 4.4). The distributions of these metrics were not formally tested due to the small sample size (James et al. 2009), but the frequencies for each metric were plotted to determine by eye if they were skewed. Values for each of the metrics were compared between unflanged males, flanged males and females in orangutans and males and females in chimpanzees using node-level ANOVAs and node-level t-tests to determine if there was a significant difference in centrality scores between the age/sex classes. Ten thousand permutations were performed for each test in UCINET (Borgatti et al. 2002). Bonferroni corrections were not applied to the results as this inflates Type II statistical errors (Moran 2003, Nakagawa 2004).

Table 4.3: Definitions of binary individual metrics (¹Croft et al. 2008, ²Opsahl et al. 2010, ³Newman 2003b, ⁴Bonacich 1987)

Binary individual metric	Definition
Degree centrality ¹	Degree centrality is the number of nodes that an individual is connected to in the network.
Closeness centrality ^{1, 2}	<p>Closeness centrality is the inverse of the sum of mean shortest path lengths between an individual and all other nodes in the network.</p> $Closeness_i = \frac{1}{\sum_j d_{ij}}$ <p>where d_{ij} is the shortest path between nodes i and j. Closeness centrality ranges from 0 to 1.</p>
Betweenness centrality ^{1, 3}	<p>Betweenness centrality is a measure of the number of shortest paths on which a node lies.</p> $Betweenness_i = \sum_{j < k} \frac{g_{jk}(n_i)}{g_{jk}}$ <p>where g_{jk} is the number of shortest paths linking nodes j and k.</p>
Eigenvector centrality ⁴	<p>Eigenvector centrality incorporates both the number of connections held by a node and the number of connections held by the node's neighbours. An individual with high eigenvector centrality is connected to a lot of nodes who also have a lot of connections.</p> $e_i = \frac{1}{\lambda} \sum_j A_{ij} e_j$ <p>where e_i is the eigenvector centrality of node i, λ is a constant and A_{ij} is the association matrix.</p>

Table 4.4: Definitions of weighted individual metrics (¹Wasserman and Faust 1994, ²Croft et al. 2008, ³Opsahl et al. 2010, ⁴Newman 2003b, ⁵Bonacich 1987)

Weighted individual metric	Definition
Strength ^{1, 2}	<p>Node strength measures the total weight of the edges connected to a node:</p> $s_i = \sum_{j=1}^n W_{ij}$ <p>where W_{ij} represents the weight of the edge connecting nodes i and j.</p>
Weighted closeness centrality ³	<p>Weighted closeness centrality is the inverse of the sum of the weighted mean shortest path lengths between an individual and all other nodes in the network.</p> $Closeness_i = \frac{1}{\sum_j \omega d_{ij}}$ <p>where ωd_{ij} is the weighted shortest path between nodes i and j.</p>
Weighted betweenness centrality ^{3, 4}	<p>Weighted betweenness centrality is a measure of the number of weighted shortest paths on which a node lies.</p> $Betweenness_i = \sum_{j < k} \frac{\omega g_{jk}(n_i)}{\omega g_{jk}}$ <p>where ωg_{jk} is the number of weighted shortest paths linking nodes j and k.</p>
Weighted eigenvector centrality ⁵	<p>Weighted eigenvector centrality incorporates both the strength of connections held by a node and the strength of connections held by the node's neighbours. An individual with high weighted eigenvector centrality is strongly connected to a lot of nodes who also have a lot of strong connections.</p> $we_i = \frac{1}{\lambda} \sum_j A_{ij} we_j$ <p>where we_i is the weighted eigenvector centrality of node i, λ is a constant and A_{ij} is the association matrix.</p>

4.2.9 Random and targeted removals

Random and targeted removals were performed on both the binary and the weighted networks for orangutans and chimpanzees. For the binary networks, 20 individuals were randomly removed in a stepwise fashion. After each removal, the mean shortest path length, the size of the largest cluster and the mean size and number of isolated clusters were recorded (Lusseau 2003). This analysis was repeated 10,000 times and the values for each network metric averaged over the 10,000 simulations for each removal. Targeted removals were then performed. The individuals with the highest degree were removed in stepwise fashion and the mean shortest path length, the size of the largest cluster and the mean size and number of isolated clusters calculated after each removal. Again, 20 individuals were removed in total. This analysis was then repeated but the individuals with the highest betweenness, closeness and eigenvector centrality were removed in descending order. These analyses were performed on both the orangutan and the chimpanzee networks.

The removal simulations were then performed on the weighted network. The procedure for random removals remained as above, with the exception that the mean shortest path length was replaced with its weighted counterpart; mean weighted shortest path length. The measure incorporates edge weight by allocating a cost to each edge based on weight; edges with high association indices are given a low cost and those with low association indices a high cost. This is achieved by simply inverting the edge weight. The mean weighted shortest path length is then calculated using Dijkstra's algorithm (Dijkstra 1959, Newman 2001). The major advantage of this method in comparison to the binary measure is that the inclusion of edge weights provides additional information about how cohesive the group actually is. However, the values produced are difficult to

interpret. Consequently, the weighted mean shortest path length was normalised by dividing it by the inverse of the average edge weight in the complete network. This means that one unit of mean weighted shortest path length represents one step of average edge weight in the original complete network (Opsahl et al. 2010). Targeted removals were again performed as above, but individuals with the highest strength, weighted betweenness, weighted closeness and weighted eigenvector centrality were removed, and the mean weighted shortest path length was calculated for the resulting networks. For the orangutan network, only 18 individuals had non-zero weighted betweenness values and so only these 18 were removed. These analyses were all performed using R (R Development Core Team 2011) with the packages igraph (Csardi and Nepusz 2006) and tnet (Opsahl 2009).

The individuals targeted are likely to be the same or similar in each of the above simulations. This is because individuals that are central in the network are likely to have high scores for all four metrics, and binary measures will probably correlate quite strongly with weighted measures. However, although there will be strong similarities in the top 20 individuals selected for removal, the order in which they are removed is likely to vary, dependent on the measure chosen. In addition, even small differences in the identities of the removed individuals may have important consequences for network fragmentation; therefore it is interesting to simulate the removal of all classes of central individuals. This may highlight which measure would be the most useful for identifying individuals for vaccination (i.e. the measure that leads to the greatest network fragmentation).

4.3 Results

4.3.1 *Network properties: orangutan binary network*

Nine orangutans were not connected to the main component. Two of these isolates were females and the other seven were males (three flanged males and four unflanged males) suggesting that males may be more likely to be isolates. These isolates were removed from the network for all following analyses.

The mean degree of the orangutan network was 7.622. The density of the network was 0.212. The network can therefore be viewed as a relatively sparse network as of all possible connections (666) only 21.2% were present (141). The diameter of the network was four, indicating that the longest distance between any two animals in the network was four edges. The clustering coefficient and the mean path length of the binary network did not differ from those of random networks (Table 4.5); therefore the network did not exhibit small-world properties (i.e. low path length combined with high clustering coefficient). The orangutans did not appear to assort by degree; in fact the correlation was in the opposite direction indicating that those with the highest degree associated with those with low degrees. This correlation, however, did not differ significantly from that expected from random networks (Table 4.5).

Table 4.5: Observed network properties from the binary orangutan network with the mean and standard deviation of the values from 10,000 randomisations of the network and the associated P values.

Network metric	Observed	Mean from randomised networks (SD)	P value
Clustering coefficient	0.377	0.354 (0.016)	0.128
Mean shortest path	1.974	1.938 (0.025)	0.174
Assortativity by degree	-0.261	-0.298 (0.031)	0.119

4.3.2 Network properties: orangutan weighted network

The weighted network is displayed in Figure 4.2. The mean strength was 0.072. The network was not small-world as the weighted clustering coefficient was significantly lower than random. The weighted mean shortest path length was higher than random and this difference was close to being significant. The network was negatively assorted by strength but this did not differ from that expected from the random networks, although again the difference was close to being significant (Table 4.6).

Table 4.6: Observed network properties from the weighted orangutan network with the mean and standard deviation of the values from 10,000 randomisations of the network and the associated P values. Bold values indicate that observed metrics were significantly different from random.

Network metric	Observed	Mean from randomised networks (SD)	P value
Weighted clustering coefficient	0.152	0.354 (0.030)	P<0.001
Weighted mean shortest path	7.859	4.157 (1.800)	P=0.055
Weighted assortativity by strength	-0.248	-0.176 (0.053)	P=0.078

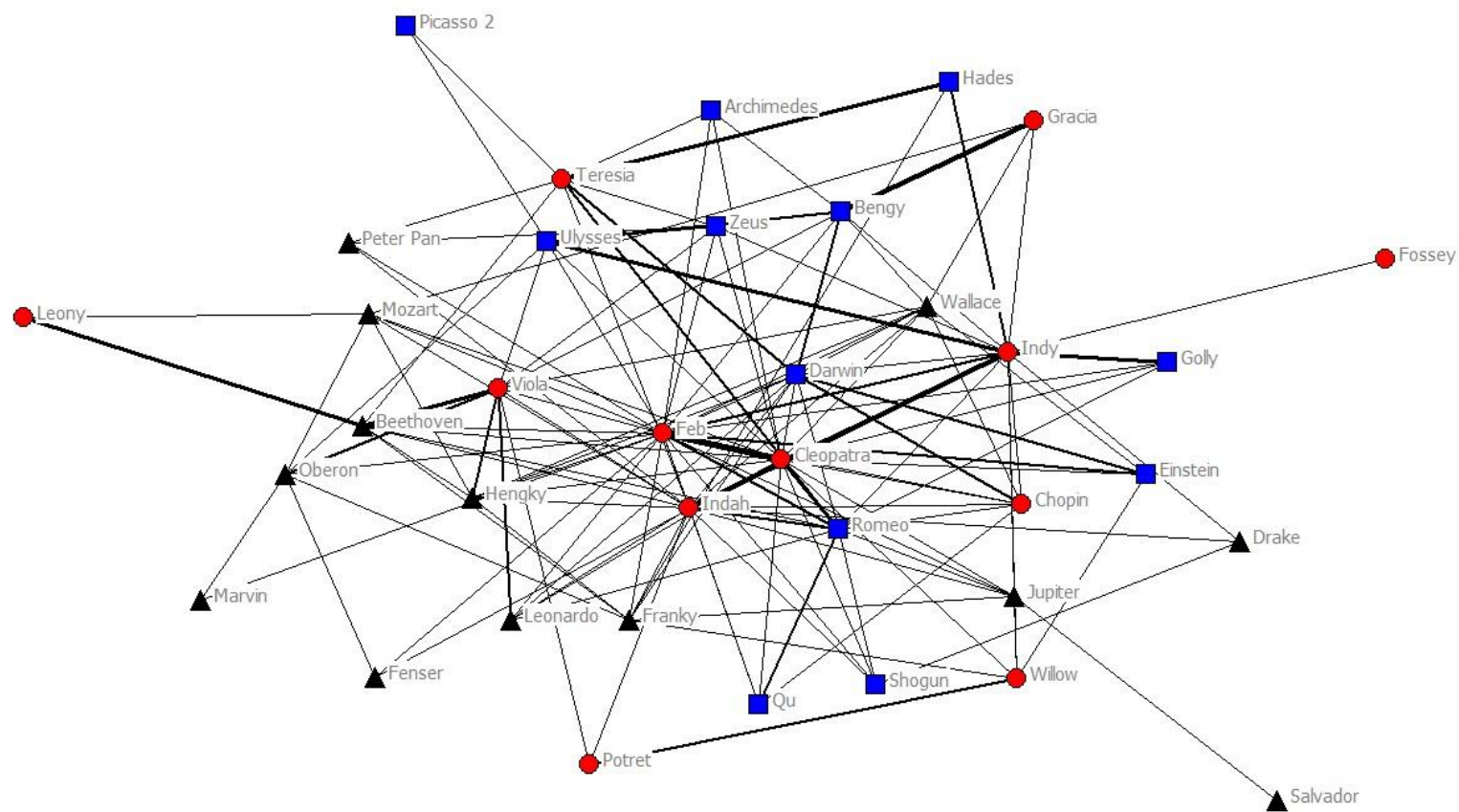


Figure 4.2: Spring-embedded sociogram of the orangutan weighted network (red circles are females, blue squares are unflanged males and black triangles are flanged males). Edge thickness indicates the strength of the relationships.

4.3.3 Network properties: chimpanzee binary network

All of the 55 chimpanzees were connected into one component. The mean degree was 49.745 and the density 0.921. The network is therefore very dense; of all possible connections (1485) 92.1% were present (1368). The diameter of the network was two. The clustering coefficient was significantly higher than expected while the mean path length did not differ from random networks (Table 4.7); therefore the network exhibited small-world properties. The chimpanzee network showed evidence of disassortative mixing, but significantly less than would be expected by random chance (Table 4.7).

Table 4.7: Observed network properties from the binary chimpanzee network with the mean and standard deviation of the values from 10,000 randomisations of the network and the associated P values. Bold values indicate that observed metrics were significantly different from random.

Network metric	Observed	Mean from randomised networks (SD)	P value
Clustering coefficient	0.941	0.939 (0.0003)	< 0.001
Mean shortest path	1.079	1.079 (0.0000)	1
Assortativity by degree	-0.171	-0.183 (0.003)	< 0.001

4.3.4 Network properties: chimpanzee weighted network

The chimpanzee weighted network is displayed in Figure 4.3. The mean strength was 5.345. The clustering coefficient was significantly lower than that expected while the mean shortest path length was significantly higher than random. Assortativity by strength was significantly lower than random, indicative of significant disassortative mixing (Table 4.8).

Table 4.8: Observed network properties from the weighted chimpanzee network with the mean and standard deviation of the values from 10,000 randomisations of the network and the associated P values. Bold values indicate that observed metrics were significantly different from random.

Network metric	Observed	Mean from randomised networks (SD)	P value
Clustering coefficient	0.327	0.939 (0.002)	<0.001
Mean shortest path	2.171	0.658 (0.004)	<0.001
Assortativity by strength	-0.134	-0.069 (0.015)	<0.001

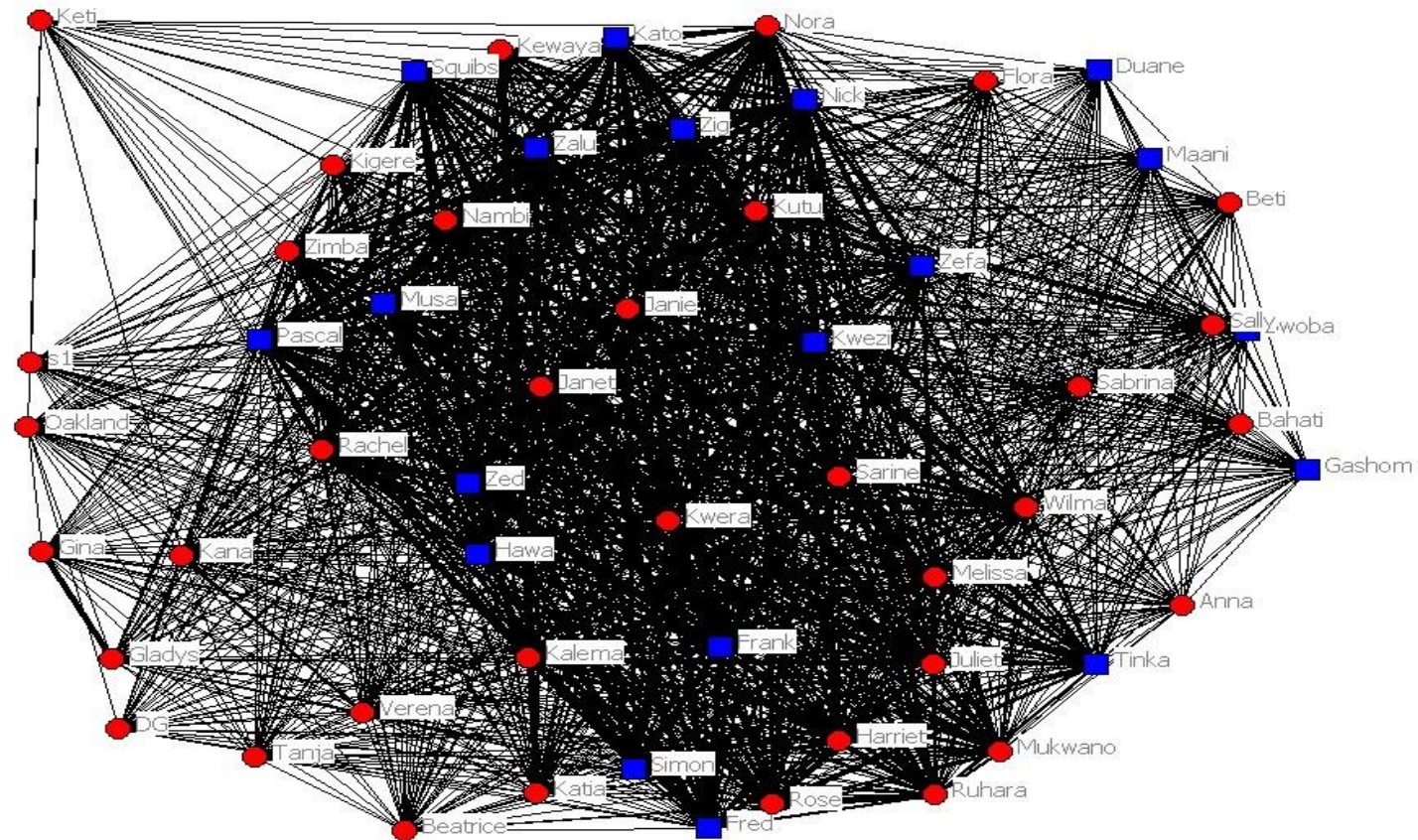


Figure 4.3: Spring-embedded sociogram of the chimpanzee weighted network (red circles are females and blue squares males). Edge thickness indicates the strength of the relationships.

4.3.5 Individual properties: orangutan binary network

The distribution of values was skewed for all four binary centrality measures in the orangutan network. For degree, closeness, betweenness and eigenvector centrality, the majority of individuals had low to medium values while only a few individuals had considerably higher scores, although this was less pronounced for closeness and eigenvector centrality (Figure 4.4). The highest four values were scored by the same four individuals (Feb, Cleopatra, Indah and Indy) for three of the centrality measures; degree, closeness and betweenness centrality (Appendix C). These individuals were all resident females (residents were individuals that were estimated to spend more than 50% of their time in the study area). The highest four scores for eigenvector centrality were scored by Feb, Cleopatra, Indah and Darwin. Feb scored the highest value for all four measures. These individuals can be viewed as potential superspreaders and may be particularly important for disease transmission in the network.

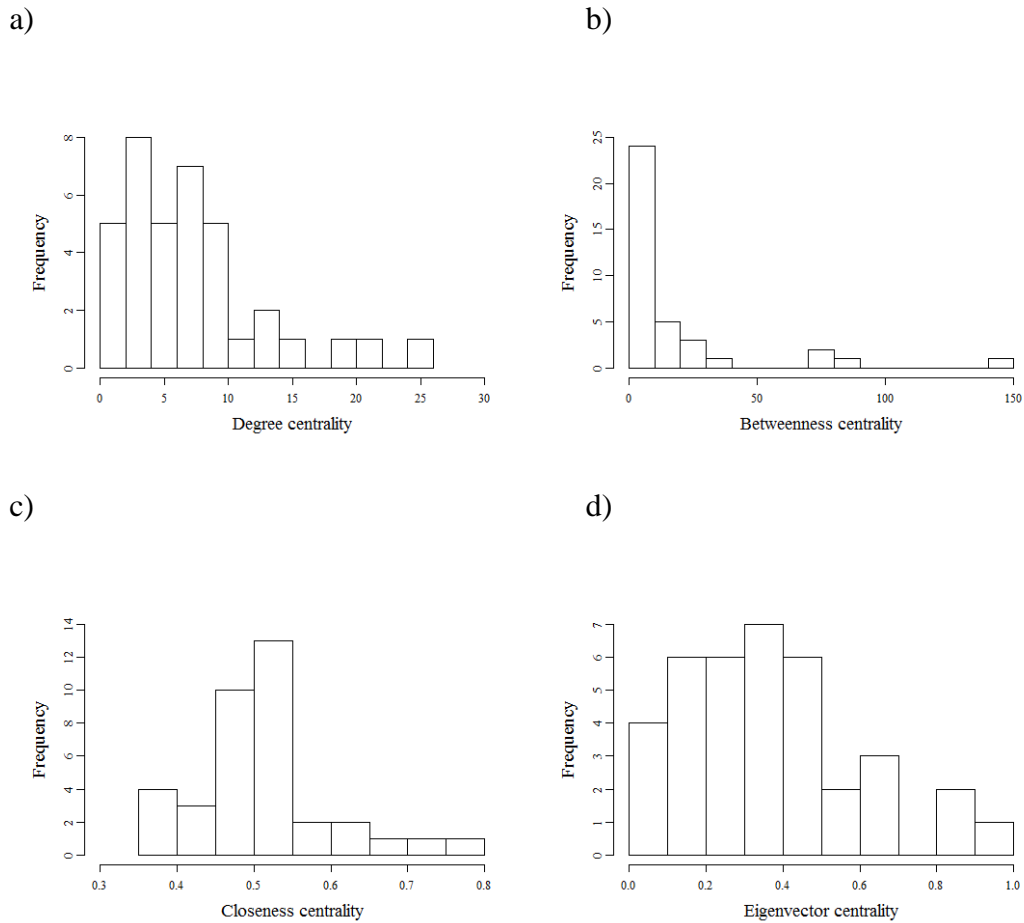


Figure 4.4: The distribution of a) degree, b) betweenness, c) closeness, and d) eigenvector centrality scores in the orangutan binary network

The values for each of the above four metrics were then compared between unflanged males, flanged males and females using node-level one-way ANOVAs in UCINET, using 10,000 permutations. There was a significant effect of age/sex class on betweenness centrality but not on degree, closeness or eigenvector centrality (Table 4.9). To determine which classes differed significantly, node-level permutation t-tests were performed using UCINET (Figure 4.5). Unflanged males and flanged males did not differ significantly in degree ($P = 0.763$), betweenness ($P = 0.492$), closeness ($P = 0.597$) or eigenvector ($P = 0.713$) centrality. Females had significantly higher betweenness than unflanged males ($P < 0.05$) but did not differ significantly in degree ($P = 0.132$), closeness ($P = 0.359$) or eigenvector ($P = 0.325$) centrality. Finally, females

did not differ significantly from flanged males in degree ($P = 0.075$), betweenness ($P = 0.052$), closeness ($P = 0.359$) or eigenvector ($P = 0.201$) centrality.

Table 4.9: Results of node-level ANOVAs for age/sex class differences in orangutan binary measures of centrality (bold values indicate a significant effect of sex class on network metrics).

	F	Df	P
Degree	2.630	2	0.084
Betweenness centrality	4.278	2	<0.05
Closeness centrality	1.128	2	0.336
Eigenvector centrality	1.159	2	0.324

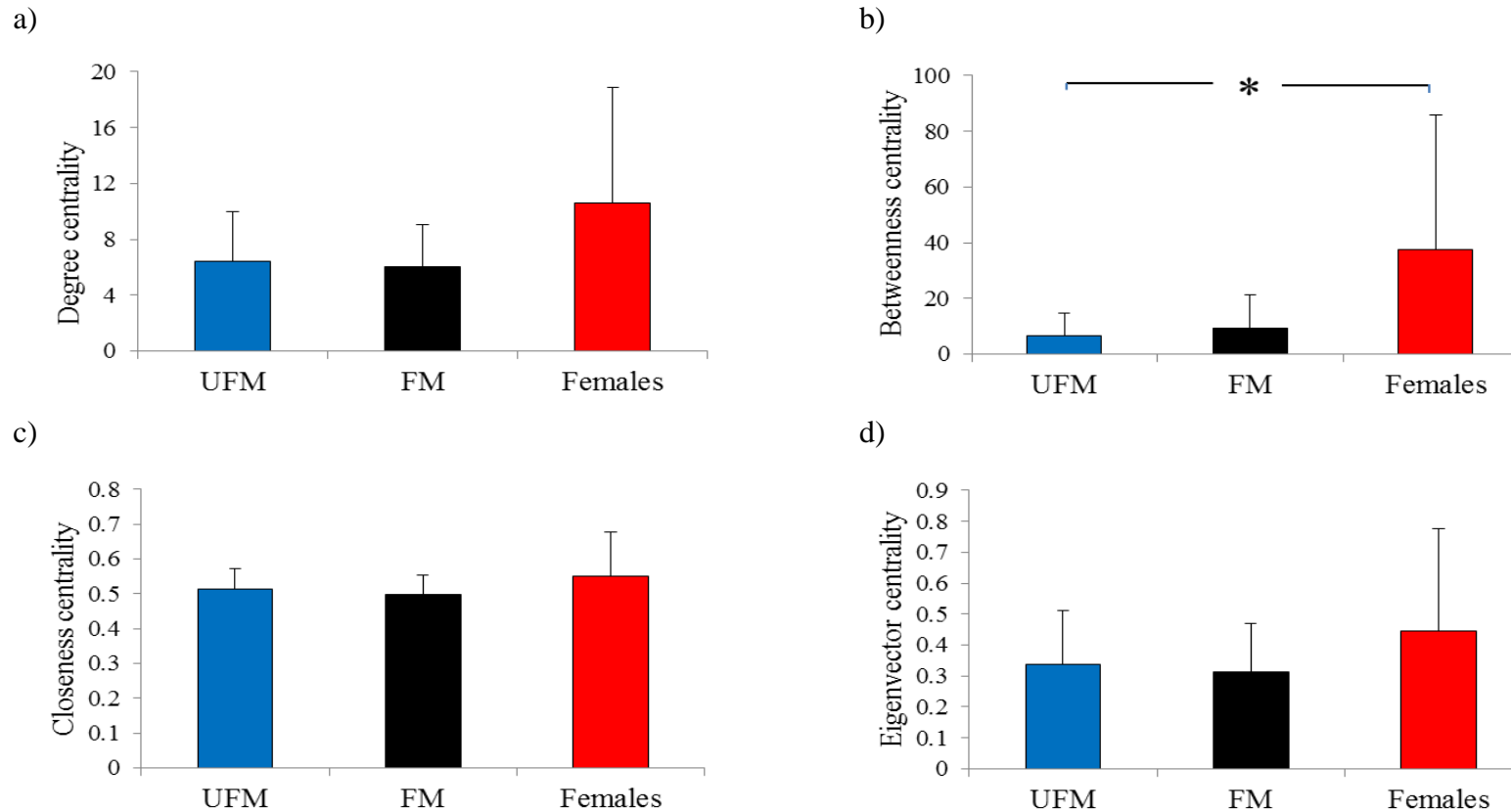


Figure 4.5: The a) degree, b) betweenness, c) closeness and d) eigenvector centrality for unflanged males (UFM), flanged males (FM) and females in the binary network. Bars represent mean values, plus one standard deviation, and * indicates $P < 0.05$.

4.3.6 Individual properties: orangutan weighted network

Similar to the binary network, the distribution of individual scores was positively skewed for strength, weighted betweenness and weighted eigenvector centrality but negatively skewed for weighted closeness centrality (Figure 4.6). The scores for weighted closeness centrality indicate that a few individuals had a considerably lower weighted closeness centrality than the majority of the other group members. Four individuals had particularly low weighted closeness centrality scores: Salvador, Drake, Fossey and Marvin (Appendix D). These individuals can be considered more peripheral individuals once the strength of relationships is taken into account. Three individuals had particularly high strength; Indy, Feb and Cleopatra. The individual with the highest strength was Indy, an adolescent resident female. There were only two individuals with particularly high betweenness values once weights were taken into account and these were Feb and Indy, with Indy again achieving the highest score. Finally, for eigenvector centrality three individuals achieved particularly high weighted values and these were Feb, Cleopatra and Indy. Indah and Romeo also had much higher eigenvector centrality scores than the rest of the orangutans, although not as high as Feb, Cleopatra and Indy.

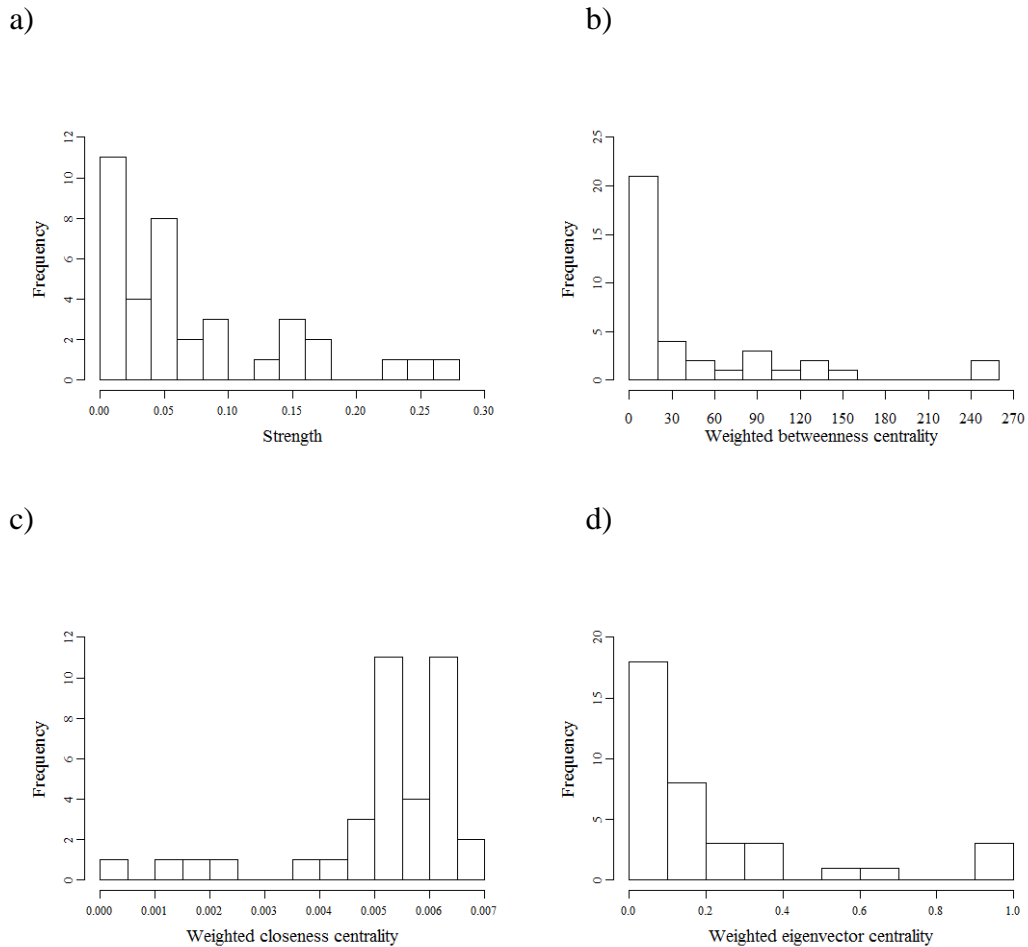


Figure 4.6: The distribution of a) strength, b) weighted betweenness c) weighted closeness and d) weighted eigenvector centrality scores in the orangutan weighted network

The values for each of the above four metrics were then compared between unflanged males, flanged males and females using node-level one-way ANOVAs in UCINET. There was a significant effect of age/sex class on strength, weighted betweenness, weighted closeness and weighted eigenvector centrality (Table 4.10). To determine which sex classes differed significantly, node-level t-tests were performed in UCINET (Figure 4.7). Unflanged males had significantly higher strength ($P < 0.05$), weighted betweenness ($P < 0.05$), weighted closeness ($P < 0.001$) and weighted eigenvector ($P < 0.001$) centrality than flanged males. Unflanged males and females did not differ significantly in strength ($P = 0.114$), betweenness ($P = 0.195$), closeness ($P = 0.400$) or

eigenvector ($P = 0.369$) centrality. Finally, females had significantly higher strength ($P < 0.001$), weighted betweenness ($P < 0.01$) and eigenvector ($P < 0.01$) centrality than flanged males, but they did not differ in closeness centrality, although this was close to significant ($P = 0.055$).

Table 4.10: Results of node-level ANOVAs for age/sex class differences in orangutan weighted measures of centrality (bold values indicate a significant effect of sex class on network metrics).

	F	Df	P
Strength	7.682	2	<0.01
Weighted betweenness centrality	4.438	2	<0.05
Weighted closeness centrality	5.662	2	<0.01
Weighted eigenvector centrality	4.834	2	<0.05

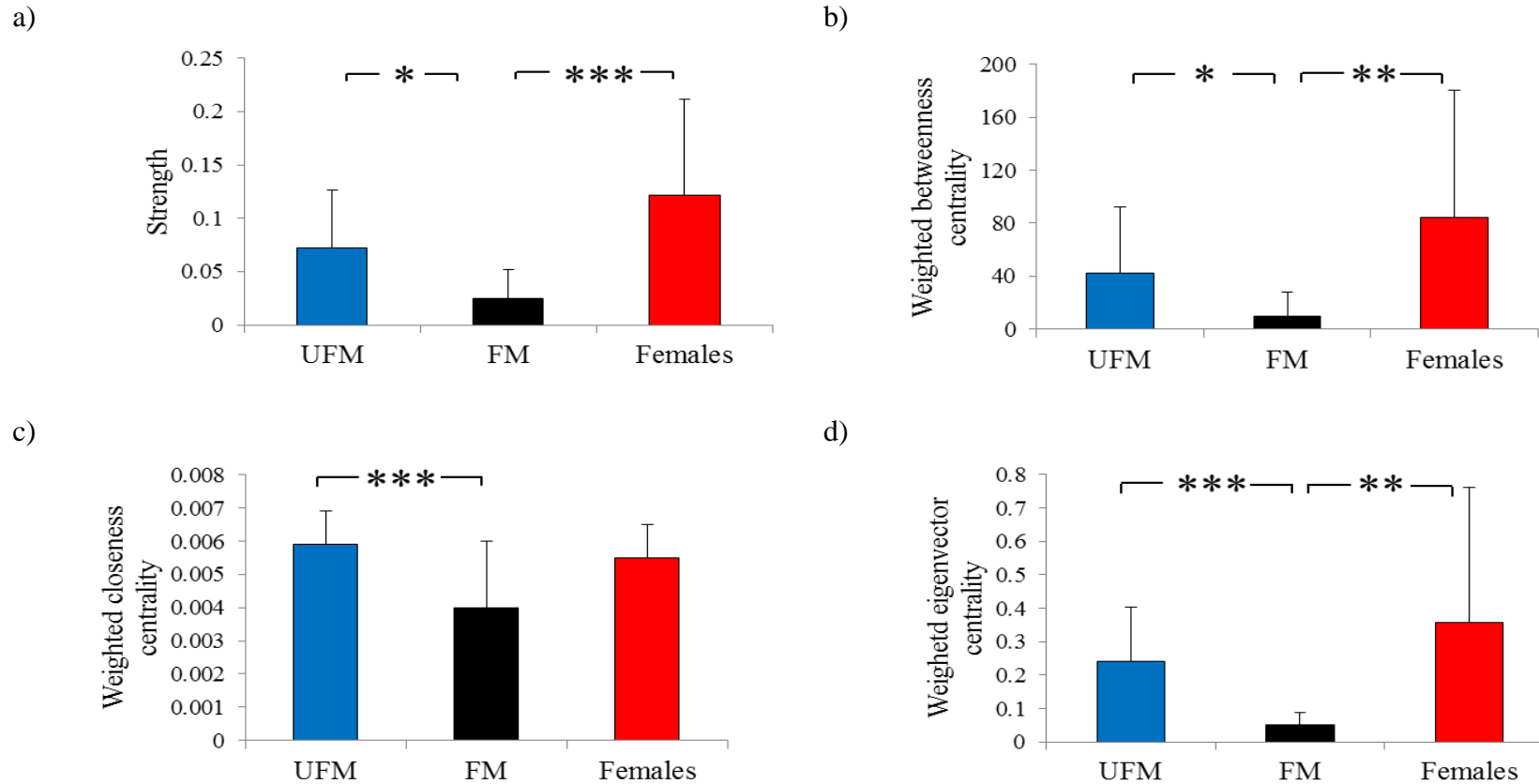


Figure 4.7: The a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality for unflanged males (UFM), flanged males (FM) and females in the weighted network. Bars represent mean values, plus one standard deviation, * indicates $P < 0.05$, ** indicates $P < 0.01$ and *** indicates $P < 0.001$.

4.3.7 Individual properties: chimpanzee binary network

The distribution of scores was skewed for all four binary centrality measures, but in the opposite direction to that found for the orangutan (Figure 4.8). A lot of individuals had very high scores for all four measures of centrality; indeed almost half of the chimpanzees in the group scored in the highest band for each measure. For degree, closeness and eigenvector centrality only one individual was characterised by very low values, Ketí, an adult female (Appendix E).

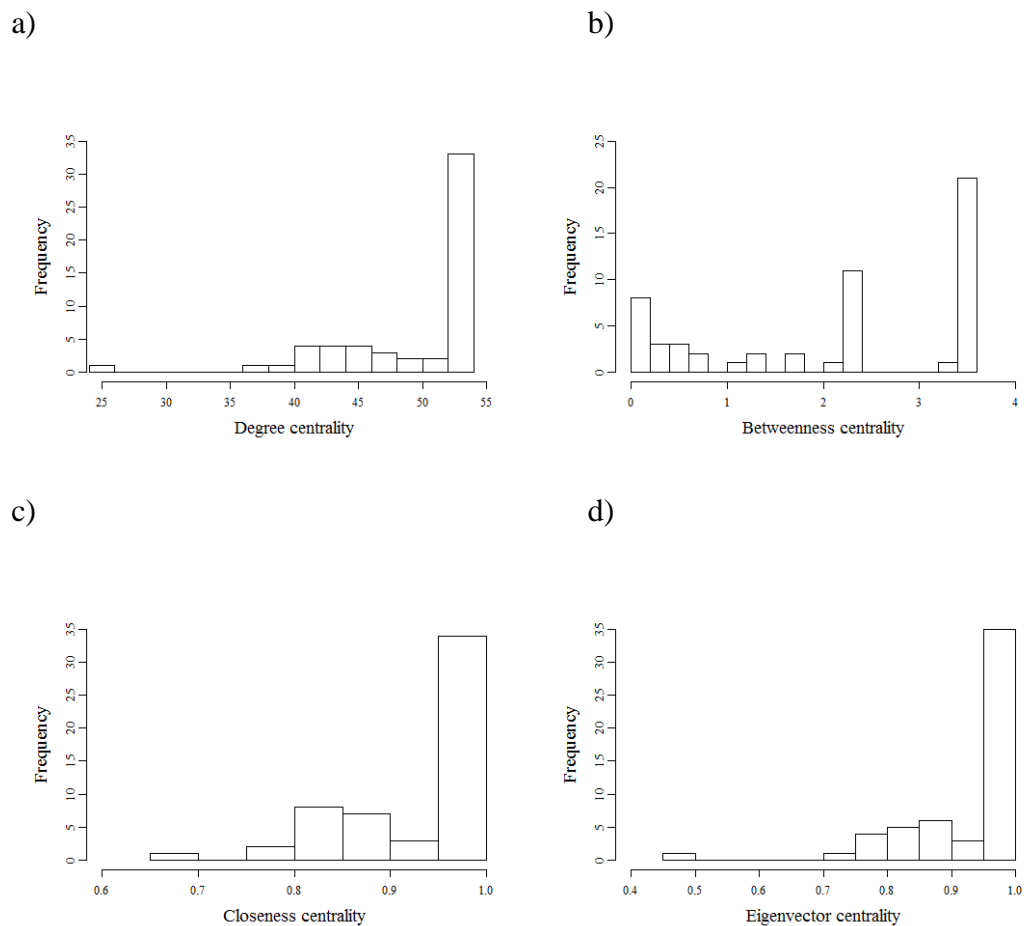


Figure 4.8: The distribution of a) degree, b) betweenness c) closeness and d) eigenvector centrality scores in the chimpanzee binary network

Node-level permutation t-tests showed that males and females did not differ significantly in degree ($P = 0.151$), betweenness ($P = 0.165$), closeness ($P = 0.136$) or eigenvector centrality ($P = 0.152$) (Figure 4.9).

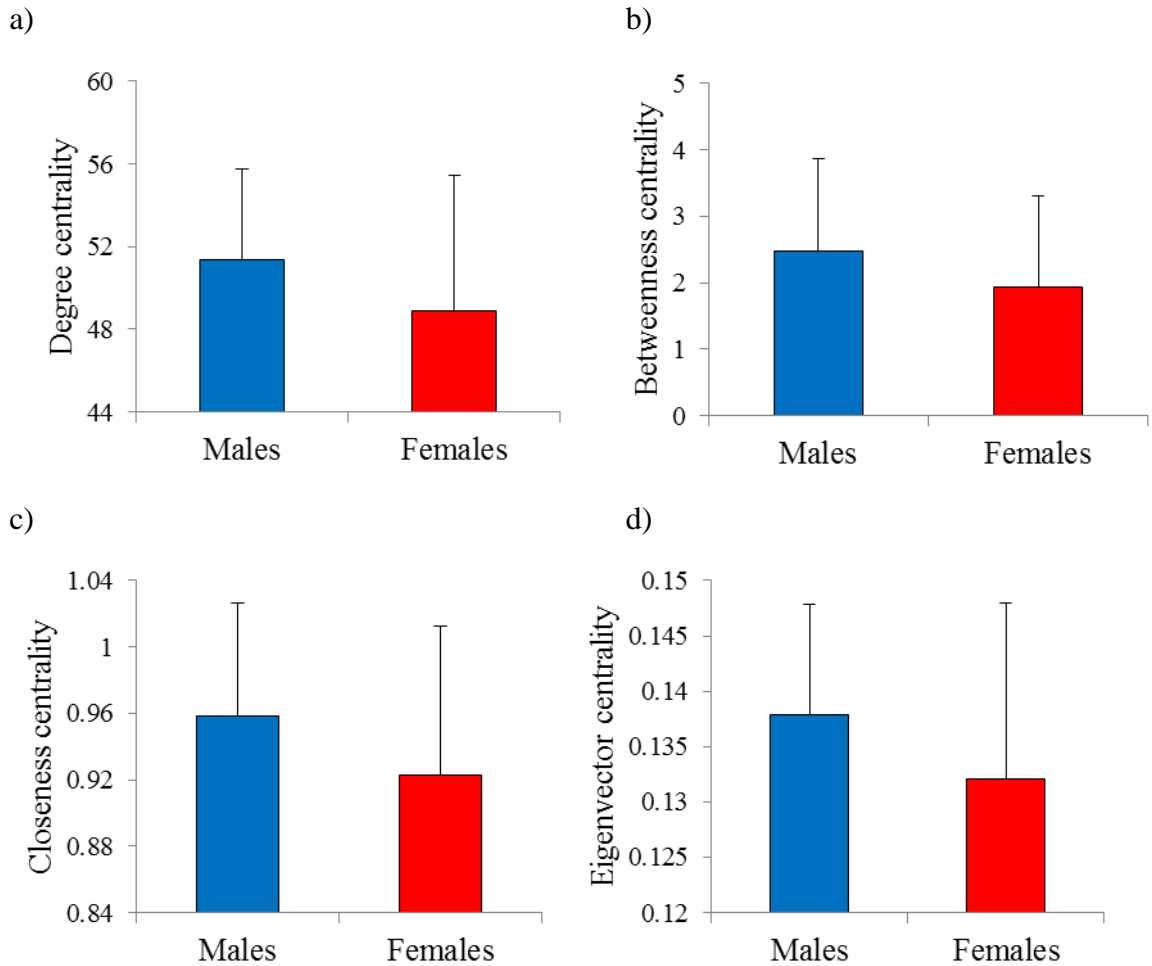


Figure 4.9: The a) degree, b) betweenness, c) closeness and d) eigenvector centrality for males and females in the binary chimpanzee network. Bars represent mean values, plus one standard deviation.

4.3.8 Individual properties: chimpanzee weighted network

The distributions of the weighted properties for strength and eigenvector centrality were not skewed (Figure 4.10). Similar to the orangutan weighted network, weighted closeness centrality was negatively skewed. Weighted betweenness centrality was the only measure that expressed some degree of positive skew, with one individual having a

considerably higher score than the rest of the group (Kutu, an adult female; Appendix F).

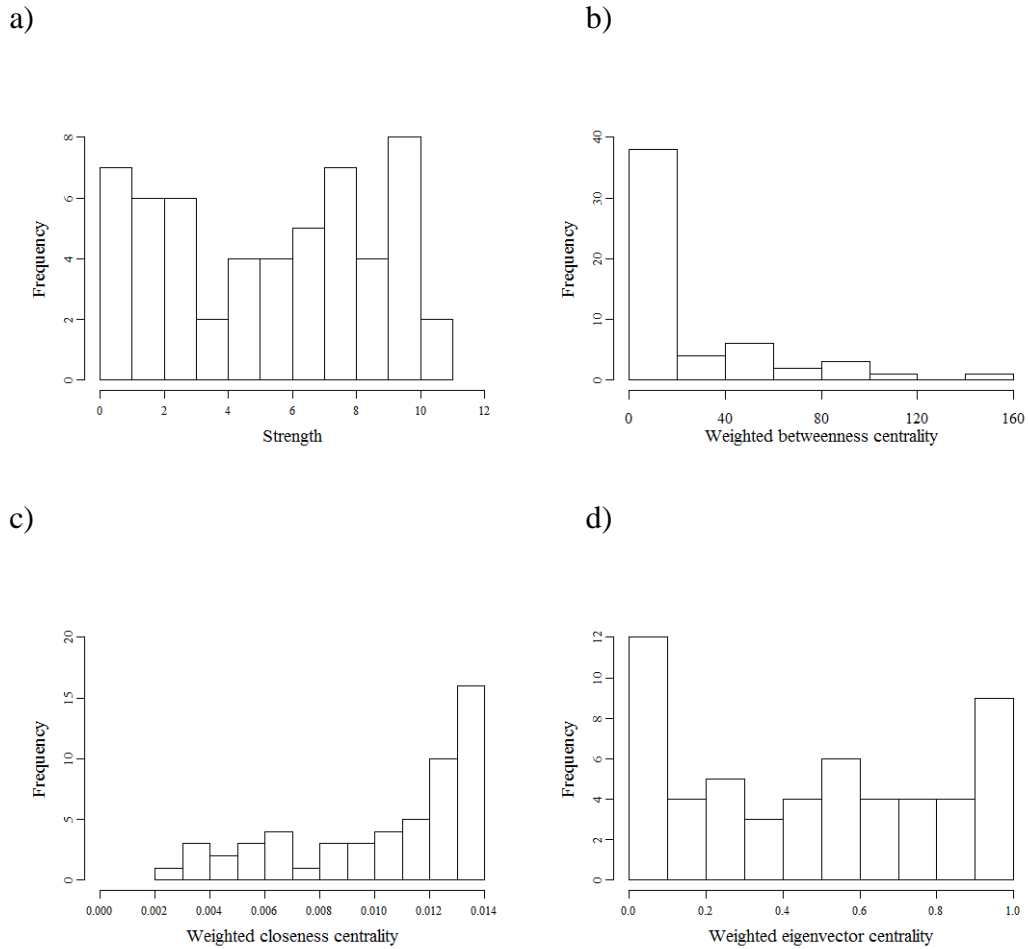


Figure 4.10: The distribution of a) strength, b) weighted betweenness c) weighted closeness and d) weighted eigenvector centrality scores in the chimpanzee weighted network

The results of the node-level permutation t-tests showed that males had significantly higher strength ($P < 0.001$), weighted closeness ($P < 0.01$) and weighted eigenvector centrality ($P < 0.001$) than females but that the sexes did not differ in weighted betweenness ($P = 0.453$) (Figure 4.11).

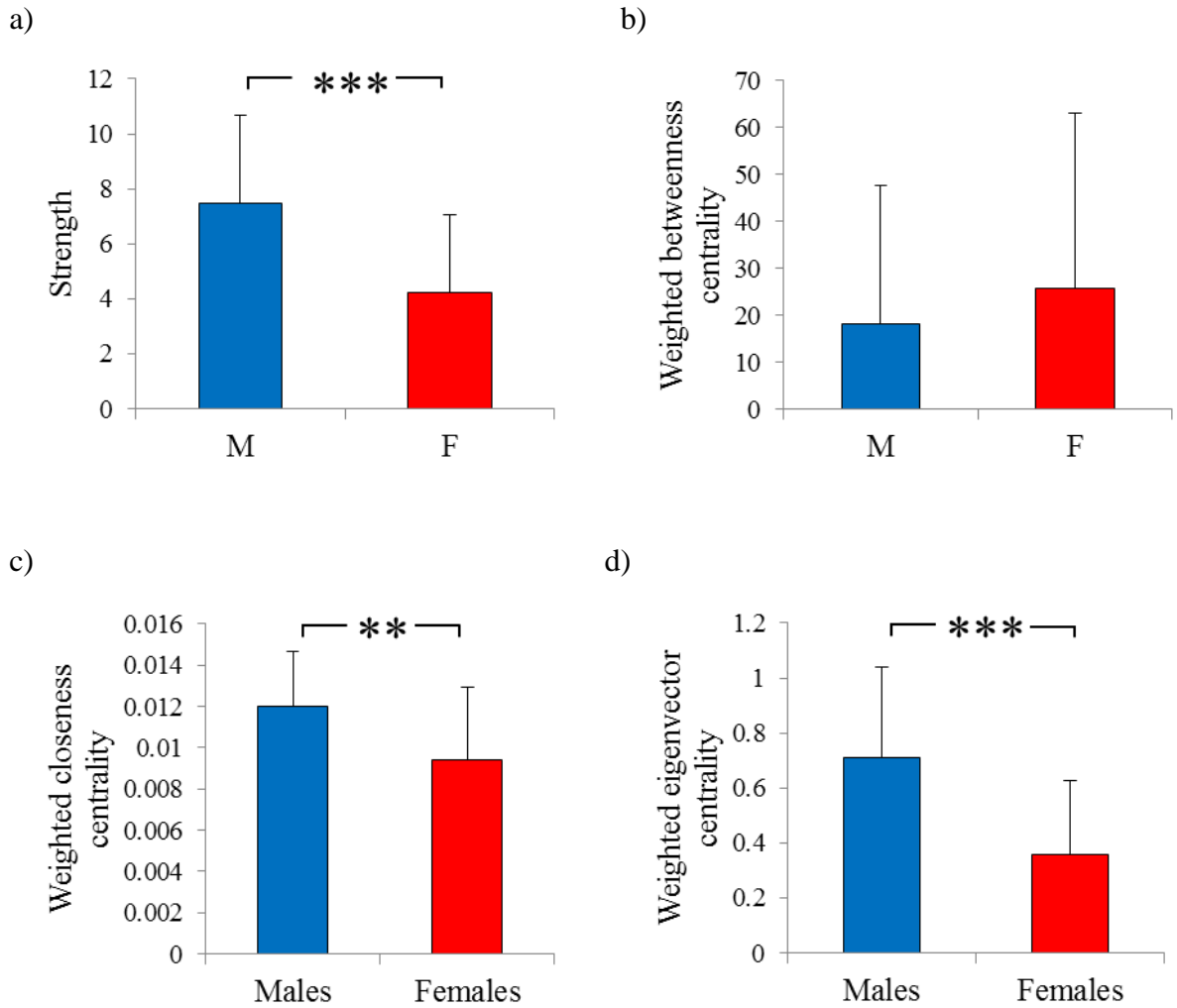


Figure 4.11: The a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality for males and females in the weighted chimpanzee network. Bars represent mean values, plus one standard deviation, ** indicates $P < 0.01$ and *** indicates $P < 0.001$.

4.3.9 Random and targeted removals: orangutan binary network

The orangutan binary network proved to be more vulnerable to targeted than to random removals, supporting the potential utility of targeted vaccinations as disease prevention measures (Figure 4.12). Mean shortest path length increased faster under all targeted removals than random removals. After the first seven to 16 targeted individuals were removed, the mean shortest path length started to decrease; this was probably a result of fewer individuals being present in the largest component. The relative size of the largest

cluster (the number of individuals in the largest cluster divided by the total number of individuals remaining) decreased considerably faster under targeted removals than random removals; indeed, when animals were removed at random the size of the largest cluster did not change much at all. Under random removals most of the orangutans remained connected in one giant component even after the removal of half of the population, while under the targeted removal the network quickly fragmented. Targeted removals led to increases in the mean size and number of isolated clusters, indicating that the network was separating into multiple components. After the targeted removal of between 10 and 18 individuals, the mean size of isolated clusters started to decrease. This is probably related to the small number of remaining individuals in the network, or the removal of individuals from the isolated clusters, reducing their size. Under random removals, the mean size of isolated clusters never exceeded one, indicating that the network never fragmented into separate components. The number of isolated clusters did not increase much under random removals, while under targeted removals this parameter increased considerably. The network therefore clearly becomes less connected and cohesive under targeted removals compared to random removals.

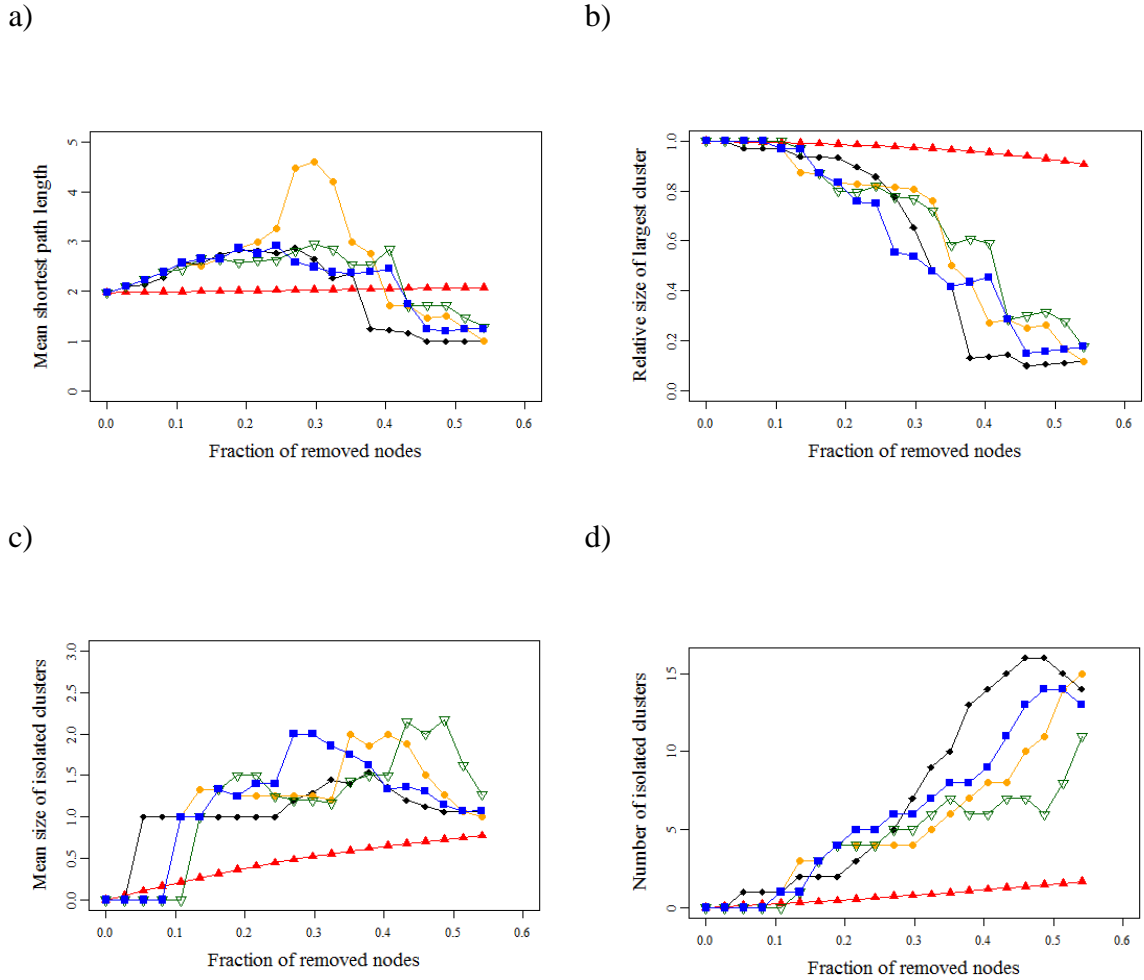


Figure 4.12: a) Mean shortest path length, b) the relative size of the largest cluster, c) the mean size of isolated clusters and d) the number of isolated clusters of the orangutan binary network with the fraction of removed nodes. Red triangles represent random removals (average of 10,000 simulations), blue squares targeted removals of individuals with the highest degree, black diamonds highest betweenness, yellow circles highest closeness and green inverted triangles highest eigenvector centrality.

4.3.10 Random and targeted removals: orangutan weighted network

The results following the removals from the orangutan weighted network (Figure 4.13) were similar to those from the binary network. The targeted removal of individuals with high strength, weighted betweenness, weighted closeness and weighted eigenvector centrality led to much greater fragmentation than random removals. This suggests that

targeted vaccinations may be a more effective preventative measure than those performed at random.

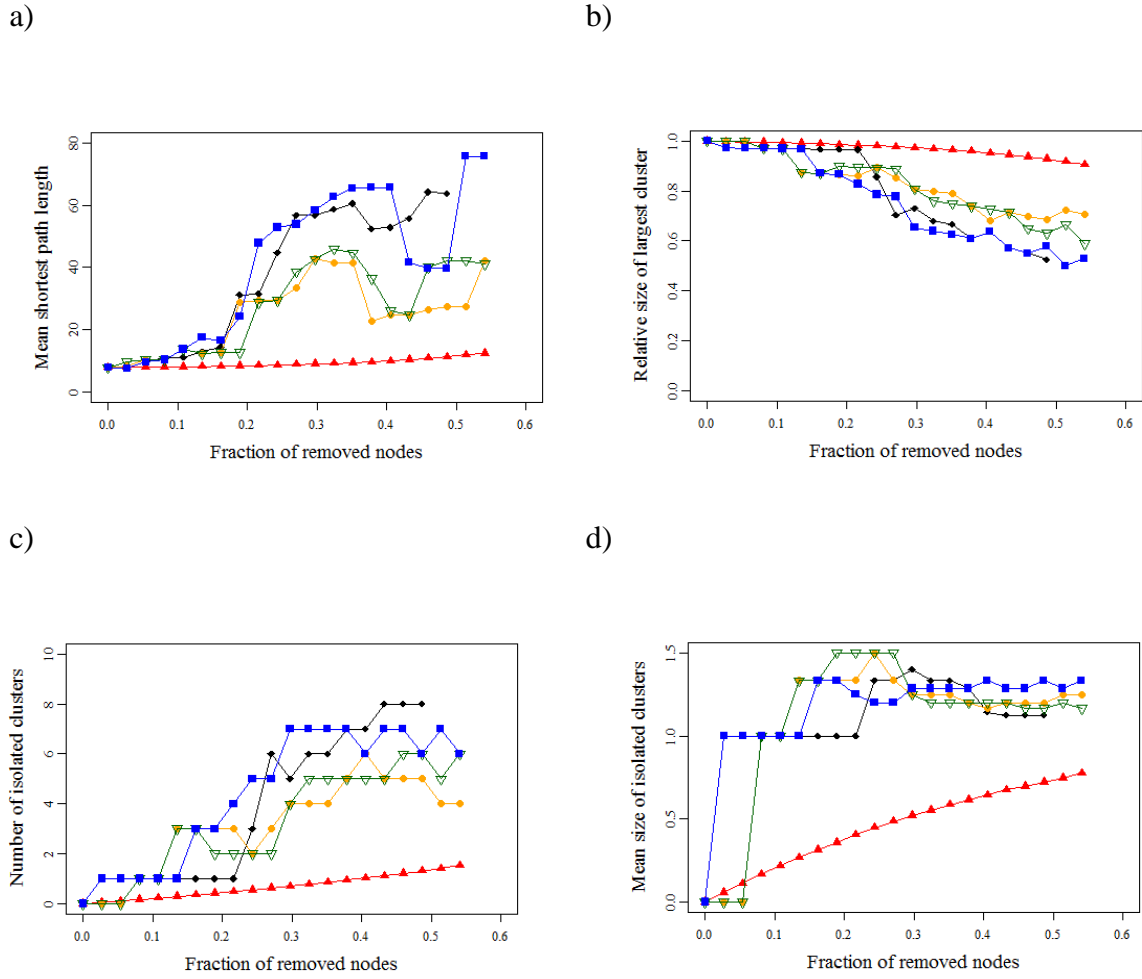


Figure 4.13: a) The weighted mean shortest path length, b) the relative size of the largest cluster, c) the mean size of isolated clusters and d) the number of isolated clusters in the orangutan weighted network with the fraction of removed nodes. Red triangles represent random removals (average of 10,000 simulations), blue squares targeted removals on individuals with the highest strength, black diamonds high weighted betweenness, yellow circles high weighted closeness and green inverted triangles high weighted eigenvector centrality.

4.3.11 Random and targeted removals: chimpanzee binary network

The 20 individuals with the highest degree in the chimpanzee binary networks were also the 20 individuals with the highest betweenness, closeness and eigenvector centrality.

All 20 individuals had exactly the same value for each metric, and so for the targeted

removals individuals were removed in alphabetical order. The network was slightly more vulnerable to targeted than to random removals (Figure 4.14). This indicates that although the chimpanzee binary network is more susceptible to targeted than random removals, it is relatively robust to both. As the first 20 targeted individuals were removed, the mean shortest path length increased faster than after random removals. The relative size of the largest cluster did not change at all under either random or targeted removals. This means that even after the removal of 20 individuals all of the chimpanzees remained connected in one giant component. As all individuals remained connected, the mean size and number of isolated clusters remained zero for all removals.

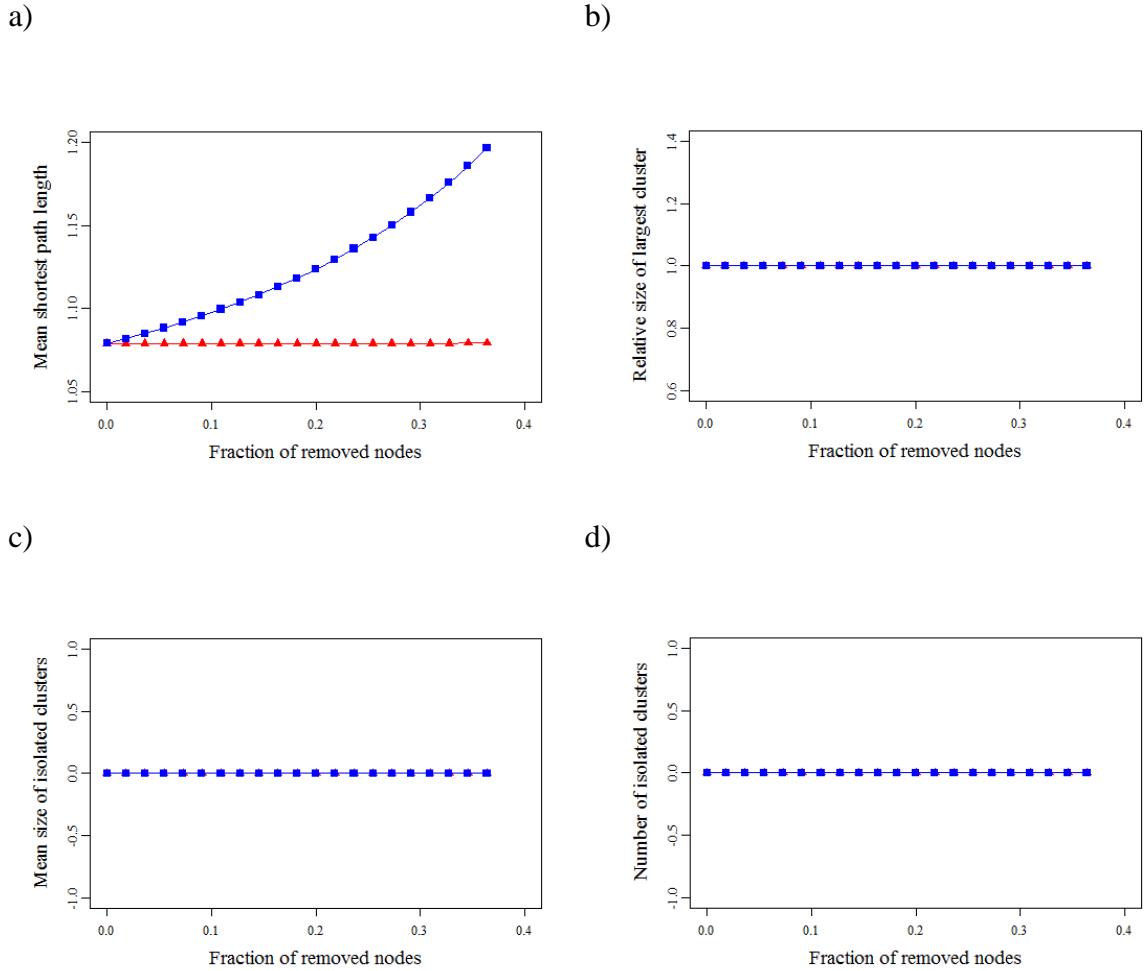


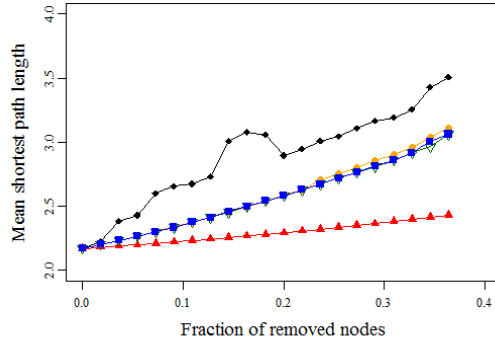
Figure 4.14: a) The mean shortest path length, b) the relative size of the largest cluster, c) the mean size of isolated clusters and d) the number of isolated clusters of the chimpanzee binary network with the fraction of removed nodes. Red triangles represent random removals (average of 10,000 simulations) and blue squares targeted removals of individuals with the highest degree/betweenness/closeness/eigenvector centrality. Where only blue squares are visible, values are the same for both random and targeted removals.

4.3.12 Random and targeted removals: chimpanzee weighted network

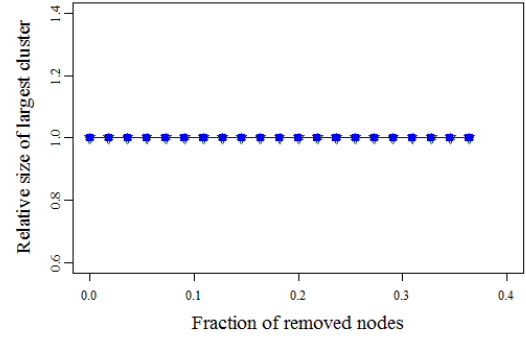
Following targeted removals on the chimpanzee weighted network the weighted mean shortest path length increased more than under random removals, and increased the most following the removal of individuals with high weighted betweenness (Figure 4.15). The relative size of the largest cluster did not change following either form of

removal; all individuals remained in one cohesive component. Consequently, the mean size of isolated clusters and the number of isolated clusters remained zero.

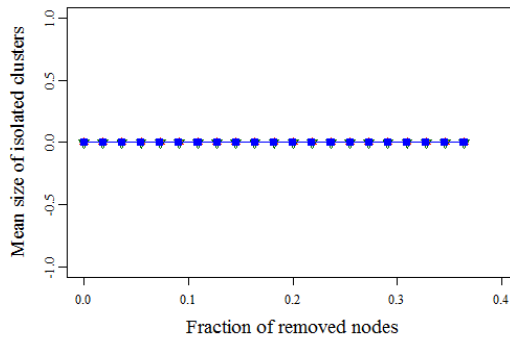
a)



b)



c)



d)

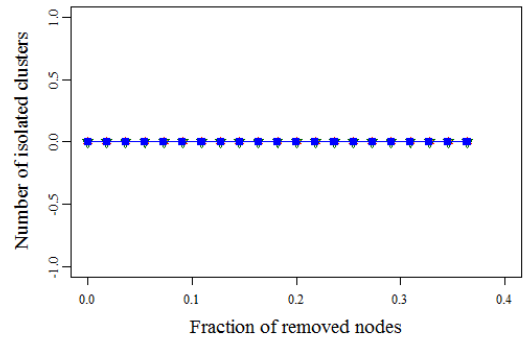


Figure 4.15: a) The weighted mean shortest path length, b) relative size of the largest cluster, c) mean size of isolated clusters and d) number of isolated clusters in the chimpanzee weighted network with the fraction of removed nodes. Red triangles represent random removals (average of 10,000 simulations), blue squares targeted removals on individuals with the highest strength, black diamonds highest weighted betweenness, yellow circles highest weighted closeness and green inverted triangles highest weighted eigenvector centrality. Where only blue squares are visible, values are the same for both random and targeted removals.

4.4 Discussion

Properties of the ape networks were shown to have potentially important implications for disease transmission. The orangutan network had a relatively low degree, diameter,

strength and density. The chimpanzee network, in contrast, had a very high degree, strength and density but also had a low diameter. Only the binary chimpanzee network was shown to have small-world properties; the orangutan networks did not have small-world properties as although the path length was suitably small, the clustering coefficient was also small. Both orangutan and chimpanzee networks were negatively assorted, indicating that highly gregarious animals preferentially associated with less social individuals. Potential superspreaders were clearly identifiable in the orangutan network, and females and unflanged males were found to be more sociable than flanged males. Among chimpanzees, males were the more gregarious sex, but potential superspreaders were not evident. Overall, both orangutan and chimpanzee networks appeared more susceptible to the targeted removal of individuals with both high degree and betweenness than to the removal of random individuals, but in orangutans this effect was considerably stronger than in the chimpanzee network. These results suggest that both orangutans and chimpanzees are vulnerable to disease spread but that in orangutans at least the targeted vaccination of central individuals may be an effective preventative strategy.

4.4.1 The vulnerability of the orangutan population and the chimpanzee community to disease: implications of overall network structure

Network properties indicated that both the orangutan and the chimpanzee networks were vulnerable to disease, but that potential epidemics are likely to spread faster and to a greater overall extent in the chimpanzee community than the orangutan population. Nine individuals in the orangutan population were never observed to associate with another orangutan, suggesting that these individuals would be much less likely to contract an infectious disease from another animal in the study area and also that if

infected they would be less likely to transmit disease to others. The other 37 individuals were all connected into one giant component and so despite the tendency of orangutans to spend most of their time alone (Rodman 1973, Galdikas 1985a), the few contacts that do occur are sufficient to connect most of the population, suggesting that disease could spread throughout most of the animals in this area. All of the 55 chimpanzees were also connected into one component. It should be emphasised here, however, that the data were collected over a long time period, and so over the shorter time frame of an epidemic, the entire group may not be connected, although this will clearly be less likely for the chimpanzee than the orangutan. Without data at a higher temporal resolution it is impossible to investigate if this would be the case.

The orangutan network had a relatively low mean degree and low strength compared to the chimpanzee network, indicating that orangutans do not spend a lot of time with other individuals relative to the time that they spend alone. Low strength is to be expected given the semi-solitary nature of the orangutan and may have implications for the types of the disease that would be expected to spread effectively in this population. Many diseases, for example tuberculosis, require long periods of association between hosts or repeated associations before transmission occurs, while diseases that are more virulent such as measles can be transmitted in a short time (Wey et al. 2008, WHO 2013). These results suggest that the social system of this orangutan population makes it relatively robust to diseases with low virulence which may require repeated contacts before infection but is likely to be more susceptible to highly infectious diseases.

All of the chimpanzees were connected in one giant component and an average degree of 49 suggests that almost all of the chimpanzees are directly connected to one another. This implies that the chimpanzees would be much more susceptible to diseases varying in virulence than the orangutans as a result of their higher level of sociality. These

predictions will be explored in more depth in the following chapter by modelling the spread of diseases varying in infectiousness and time to recovery across these networks using a susceptible-infected-recovered model.

The orangutan network was relatively sparse, with only 21% of possible connections present. Although it is difficult to compare densities between studies because group size and the filtering methods used to construct networks will affect the results, it is still interesting to look at the variation in values found to date. The density of the orangutan network is similar to those found for a number of other species. Leaf-roosting bat networks had densities of 0.20, 0.14 and 0.10 (Chaverri 2010), those of ground squirrels 0.12 (Manno 2008), killer whales 0.28 (Guimarães et al. 2007), pygmy bluetongue lizards 0.25 (*T. adelaidensis*; Fenner et al. 2011) and guppies 0.16 (Croft et al. 2005). The primate networks studied to date had much denser networks; behavioural networks of a group of 20 baboons ranged from 0.31 for a mounting network to 0.44 for a grooming network (Lehmann and Ross 2011), while networks from a group of 21 rhesus macaques ranged from 0.34 for a vocal exchange network to 0.66 for a proximity network (Brent 2009). Finally, the chimpanzee network analysed here had an extremely high density of 0.92. The density of the network is important with regards to disease transmission as disease is predicted to spread faster and to a greater overall extent in denser networks (Wey et al. 2008). These comparisons between species are interesting as they suggest that disease may spread slower or less completely in the orangutan network than in most other primate networks characterised by higher densities.

The orangutan network had a diameter of four, which means that any two individuals in the network could be connected by a maximum distance of only four steps. The chimpanzee network had a lower diameter of two. A killer whale network comprised of 43 individuals had a diameter of four (Guimarães et al. 2007), while rhesus macaque

grooming and vocal exchange networks of 21 females had diameters of three and the proximity network a diameter of two (Brent 2009). Again the implication is that orangutans have less cohesive groups than other primates. In terms of disease transmission, this finding indicates that disease could spread from one side of the network to the other in only four steps and that disease could potentially reach all group members quite quickly (Sueur et al. 2011). In chimpanzees, disease spread is predicted to be even quicker. However, it should be reiterated that the data were compiled over a long time period and so this may not be the case for shorter term diseases.

One of the major features of relevance for disease transmission is the ‘small-world effect’ which describes a network with high clustering and low path length in which disease is predicted to spread extremely quickly (Watts and Strogatz 1998). The orangutan network had a low path length in both the binary and the weighted networks. This indicates that on average individuals can be reached in a very short number of steps (less than two in the binary network) which implies that disease could rapidly spread throughout the network (Keeling and Eames 2005, Eames 2008). However, the network could not be said to have small-world properties as although it had a short path length, the clustering coefficient was low in both networks and in the weighted network it was significantly lower than expected based on the randomisations. This is an unusual result in comparison to other animal networks studied to date. Small-world properties have been found in bottlenose dolphins (Lusseau 2003, Lusseau et al. 2006), captive chimpanzees (Kanngiesser et al. 2011), killer whales (Guimarães et al. 2007), possums (Porphyre et al. 2008), manakins (Ryder et al. 2008), rhesus macaques (Brent 2009) and guppies (Croft et al. 2004). In addition, a human close contact (<3m) network in a school (Salathé et al. 2010) and a network of actor collaborations in films (Watts and Strogatz 1998) were found to be small-world. High clustering coefficients alone have

also been found in leaf-roosting bats (Chaverri 2010), ground squirrels (Manno 2008), onager and Grevy's zebra (*Equus hemionus khur* and *E. grevyi*; Sundaresan et al. 2007), and Tasmanian devils (*Sarcophilus harrisii*; Hamede et al. 2009). Therefore, small-world properties, and high clustering coefficients in particular, appear to be a common feature of animal networks. The binary chimpanzee network studied here also displayed small-world features; however, the weighted network did not. In fact, all of the non-human animal networks cited above that had small-world properties were also binary; therefore it is possible that this is a feature of binary networks in animals that disappears when weights are included in the analysis.

This may account for the lack of small-world properties in the weighted orangutan and chimpanzee networks, but the binary orangutan network also did not exhibit a high clustering coefficient, a key feature of small world networks. It has been suggested that high clustering coefficients result from the division of most social networks into groups or communities (Newman and Park 2003). Orangutans have a highly dispersed social structure with individuals ranging over large areas and a relatively high number of transient individuals that migrate between communities (Rijksen and Meijaard 1999). The orangutans included in this analysis were those that spent time within a 9km² region of the Sabangau National Park and included a small number of resident individuals and the transient individuals that passed through the area numbering only 46 in total. This sample is probably not large enough or taken over a large enough area to incorporate different communities, which may explain the low clustering coefficient. When a dolphin population off Australia was analysed as two separate communities, one community had a significantly lower clustering coefficient than expected while the clustering coefficient of the other group did not differ significantly from random (Wiszniewski et al. 2009). This may be the result of analysing a small subset of the

population. It would be interesting to collect data on a wider population of orangutans to determine if when analysed at this level, a higher clustering coefficient becomes apparent.

The binary and weighted orangutan and chimpanzee networks were all characterised by negative assortativity coefficients. This implies that the individuals with the most or strongest relationships preferentially interacted with those with the least or the weakest relationships (Newman 2002). The fact that the average of the random networks was also negative implies that this property is a result of the number of individuals and edges in the network and the degree distribution as these were the only features that were preserved in the randomisations. In the orangutan network, a few individuals have a lot of contacts while the majority have many less. This means that the most central individuals are indeed connected to many individuals with only a few contacts. In the chimpanzee network in contrast there are a very large number of connections and the most central individuals are connected to almost all of the other chimpanzees in the network. Again, this means that the least social animals are connected to the most social ones. These results are unusual however, as an analysis of networks based on sociopositive interactions within groups of strepsirrhines, New World and Old World monkeys found that overall there was evidence of positive assortativity by strength in 68 out of 70 networks (Kasper and Voelkl 2009). Bottlenose dolphins (Lusseau and Newman 2004) and guppies (Croft et al. 2005) have also been shown to exhibit some level of positive assortativity and human social networks are usually assortative; it is biological and technological networks that are commonly found to be disassortative (Newman 2002). The disassortativity observed here may be related to network filtering. If many of the relationships that exist between central and peripheral individuals are quite weak they will be removed from the network by filtering. Thus, networks that

have been filtered may appear more assortative than those in which all relationships are included. Nevertheless, if orangutan and chimpanzee networks are in fact disassortative this could have important implications for disease transmission. In disassortative networks, diseases can more easily spread to the whole population than in assortative networks in which diseases are more likely to become isolated and die out within cliques – although disease will spread very quickly within these cliques (Newman 2003b). Assortative networks also have more redundant links between central individuals; therefore targeted vaccinations aiming to prevent the transmission of disease by destroying network connectivity may not be very effective (Newman 2002). In contrast, in disassortative networks the removal of central individuals could effectively remove links and consequently potential disease pathways between different sections of the network (Newman 2002). Thus, the negative assortativity coefficient does suggest that disease may be able to spread throughout the ape networks but also that targeted vaccinations may be an effective preventative strategy.

4.4.2 The identification of potential superspreaders based on individual network properties

Potential superspreaders may play a disproportionately influential role in disease spread as well as incur a higher risk of infection. The identification of superspreaders may consequently be beneficial for conservation measures aiming to reduce or prevent disease spread. The presence of superspreaders is indicated by a positively skewed degree distribution. The distribution of the individual measures was highly positively skewed for three of the four centrality measures (degree, betweenness and eigenvector centrality) in both the orangutan binary and weighted networks, while closeness centrality was also slightly positively skewed in the binary network. Positively skewed

degree or strength distributions have been found in numerous animal networks studied to date, including red harvester ants (*Pogonomyrmex barbatus*; Pinter-Wollman et al. 2011), honeybees (*Apis mellifera*; Naug 2008), deer mice (Clay et al. 2009), dolphins (Lusseau 2003), ground squirrels (Manno 2008), captive chimpanzees (Kanngiesser et al. 2011), 50 out of 70 primate networks studied (Kasper and Voelkl 2009) and manakins (Ryder et al. 2008), although Tasmanian devils were not found to have a skewed degree distribution (Hamede et al. 2009). Positively skewed betweenness distributions have been found in both dolphins (Lusseau and Newman 2004) and chimpanzees (Kanngiesser et al. 2011). The chimpanzee network studied here also had a skewed weighted betweenness distribution, but none of the other measures were positively skewed. Similarly, at Kibale Forest, Uganda, Rushmore et al. (2013) found that the strength distributions in chimpanzee networks (based both on close contacts within five metres and party membership) were not skewed towards particular individuals.

There is evidence from empirical disease networks that high degree, closeness and betweenness centrality can correlate with individual infection risk (Corner et al. 2003, Godfrey et al. 2009, Drewe 2010), while high strength and betweenness have been shown to increase the ability to spread disease (Vicente et al. 2007). This finding suggests that these network properties may be accurate measures of superspreading power in animal networks. The skewed distributions in centrality measures in the orangutan network consequently indicate that there may be individuals that are both more susceptible to infection and also more likely to transmit disease, i.e. superspreaders. Among the orangutans, three individuals in particular, Feb Cleopatra and Indy who were all resident females, showed very high values for almost all centrality measures. These three individuals can therefore be viewed as possible

superspreaders and would potentially be good targets for vaccination programmes. Darwin had a very high eigenvector centrality score in the binary network while Indah and Romeo had relatively high weighted eigenvector centrality scores, and so these individuals may also be important in disease spread. Interestingly, the three individuals with the highest centrality values overall were all resident females. In addition, females overall were shown to have significantly higher strength, weighted betweenness centrality and weighted eigenvector centrality than flanged males. This indicates that females in this area are more social than flanged males. This result is not unexpected given what is currently known about the orangutan social system. Flanged male orangutans are generally intolerant of one another and their associations with females are largely related to mating opportunities (Mitra Setia et al. 2009, Utami Atmoko et al. 2009a). Unflanged males are more social but tend to become less tolerant of one another as they age (Utami Atmoko et al. 2009a). This was also reflected in the results here; unflanged males had significantly higher strength, weighted betweenness, weighted closeness and weighted eigenvector centrality than flanged males. Nulliparous sexually active females or adolescent females have been found to be the most gregarious age/sex class of orangutan (Galdikas 1985a, Mitra Setia et al. 2009), and again this was reflected in the network metrics here; the two most central individuals overall were Indy and Feb, both adolescent females. This indicates that both females and unflanged males may play important roles in disease spread in this population, but that adolescent females in particular may be more susceptible to becoming infected as well as more likely to transmit disease within the network. This result is in accordance with evidence from wild females in Sumatra which had an overall higher prevalence of gastrointestinal parasites, which may be spread by close contact, than males (Mul et al. 2007).

It is important to mention, however, the potential importance of observation bias on these results. Although the use of a weighted network based on dyadic association indices should prevent sampling bias from affecting the results, it is possible that the very strong bias in observation time towards particular individuals in the orangutan dataset could account for some of the skew in centrality measures. Two of the most central females, Feb and Indah, were also the two most frequently observed orangutans. These individuals may therefore appear to be the most central animals simply because they were observed far more often than others and so more of their social interactions were recorded. However, the third and fourth most frequently observed individuals were Hengky and Beethoven, two flanged males, who had medium to low centrality for all measures, suggesting that observation bias does not account for all of the observed individual differences in centrality.

Furthermore, a relationship between observation time and centrality is likely to be strongly influenced by the amount of time an individual spent in the study area; individuals that are more regular visitors to the study area are likely to be observed more often and to have a greater number of relationships with other orangutans in the region. This is because transient individuals are more likely to come into contact with a resident than another transient animal, who may only be in the region for a short time. Detailed data on the time each individual spent in the area were not available and so it was not possible to explore quantitatively the relationships between centrality, observation time and the time spent in the study area; however, it is interesting that the three most central individuals were all classed as residents (Morrogh-Bernard 2009). Thus, it is possible that both centrality and observation time are affected by the length of time that orangutans spend in the area, rather than that centrality is affected directly by observation time.

The chimpanzee network differed from the orangutan network in a number of ways. All of the binary network measures were negatively skewed, indicating that most chimpanzees in the community had equally high scores. This is probably a result of the long period of data collection and the decision not to filter the network. This means that in the binary network two individuals are connected even if they are only seen together once over the three year period, which leads to an almost completely connected network in such a gregarious species. Using an unfiltered binary network for chimpanzees does not appear to be a very useful technique. Alternatively, the weighted network incorporates the strength of relationships and allows for a more in-depth analysis. Strength and weighted eigenvector centrality were found to be fairly evenly distributed. There is clear variation between individuals in these measures of centrality, but not to the extent observed in the orangutan network. Only the distribution of weighted betweenness values was positively skewed, and only one individual, Kutu, an adult female, appears to have a particularly high value. This suggests that superspreaders are likely to play a less important role in disease spread among chimpanzees than among orangutans.

The chimpanzees also differed from orangutans in the role of the sexes in the network. Males were found to be the more social sex, with significantly higher scores for strength, weighted closeness and weighted eigenvector centrality. Males have also been found to be the more gregarious sex in a range of other chimpanzee studies; males were more frequently found in groups than females (Doran 1997), had a greater tendency to join groups (Chapman et al. 1995), spent less time alone (Lehmann and Boesch 2008), were involved in more grooming and social interactions than females (Sugiyama 1969) and were found to be significantly more gregarious than anoestrous females (Pepper et al. 1999). At Kibale, Rushmore et al. (2013) found that adult females and juveniles with

large families had the highest strength, but also found that high ranking males had high strength in the close contact network. In sum, male chimpanzees are therefore likely to play a more important role in disease spread than females, but the extent of this may vary between sites. This generally greater gregariousness among males may be a result of the lower costs of grouping for males. Larger groups incur greater travel costs and as females (particularly mothers) travel slower than males, the travel costs of grouping are greater (Wrangham 2000). Overall, findings indicate that while females may be the predominant sex in disease spread between orangutans, among chimpanzees it is likely to be males that have the greatest influence.

Finally, it is interesting to note that the distribution of the weighted closeness centrality scores was actually negatively skewed for both the orangutans and the chimpanzees, while binary closeness centrality was slightly positively skewed. An individual's closeness centrality is the inverse of the mean shortest path to all other nodes in the network (Croft et al. 2008) and the weighted measure simply uses weighted mean shortest paths in the calculation. High closeness centrality is associated with nodes that can reach all others in the network quickly (Opsahl et al. 2010). The different results between binary and weighted networks are interesting as they suggest that for closeness centrality, using the simplified binary network may produce misleading results. Weighted networks contain more information about the true structure of the group (Whitehead 2008) so it seems reasonable to conclude that these ape populations do not contain individuals with a considerably higher closeness than others in the network. In contrast, most nodes are actually similar in closeness. In the orangutan network, four individuals have particularly low values (Salvador, Fossey, Marvin and Drake). In the chimpanzee network, one individual has a particularly low score, DG, an adult female. These individuals can be considered to be more peripheral individuals once edge

weights have been included, and looking at the sociograms (Figures 4.2 and 4.3) this can indeed be seen to be the case. These analyses further highlight the value of using a weighted network over a binary network.

4.4.3 Assessing the utility of vaccinations and the impact of death on network topology

If great apes are exposed to a fatal and highly infectious epidemic in the future, vaccination may be one of the only measures with the potential to prevent widespread deaths. Targeted and random removals were therefore performed to simulate the vaccination of either random or highly central individuals.

For orangutans, the targeted removal of individuals with high centrality had a considerably greater effect on the mean shortest path length than random removals in both the binary and the weighted network. Greater increases in path length following targeted than random removals have also been found in ground squirrels (Manno 2008), dolphins (Lusseau 2003) and both the binary and weighted chimpanzee networks analysed here. These results have implications for disease transmission as they suggest that the removal of highly connected individuals, by increasing path length, may have a beneficial effect in slowing down the spread of disease across the orangutan network. In contrast, the high number of strong links between chimpanzees ensures that the path length remains low even after a large proportion of the community is removed. This suggests that targeted vaccinations may not be an effective strategy for chimpanzees as disease will still be able to reach all community members within a few steps.

In the orangutan network, changes to the size of clusters also indicated that the network became more fragmented under targeted than random removals. The size of the largest cluster decreased considerably more and faster while the mean size and number of isolated clusters increased much more under targeted than random removals. Similar

decreases in the size of the largest cluster and increases in the mean size of isolated clusters following targeted removals have been found in ground squirrels (Manno 2008) and captive chimpanzees (Kanngiesser et al. 2011). However, the chimpanzee network analysed here did not fragment but remained as one giant component. This network was not filtered, while the captive chimpanzee network was heavily filtered (Kanngiesser et al. 2011), which may explain these differing results. The captive chimpanzee group was also composed of only 17 individuals that were together all the time and the network was based on grooming relationships (Kanngiesser et al. 2011). The discordant results may therefore be attributed to differences in group size or the behaviour measured, or may reflect differences in behaviour between captive and wild chimpanzees as the fission-fusion behaviour is clearly constrained in captive animals. The clear fragmentation of the orangutan network following targeted removals into smaller and more isolated components suggests reduced potential for disease transmission as diseases may become isolated in the clusters in which they first appear (Sundaresan et al. 2007). In contrast, the lack of fragmentation of the chimpanzee network suggests that targeted removals, or the death of individuals, would not have such a great impact on disease spread as the group remained completely connected.

Overall, the orangutan network is clearly more vulnerable to the targeted removal of individuals with high centrality than random removals; in all simulations, random removals led to only a gradual increase in network fragmentation. These results are similar to those from previous removal simulations on different species: ground squirrels (Manno 2008), captive chimpanzees (Kanngiesser et al. 2011), killer whales (Williams and Lusseau 2006) and shark habitats (*Scyliorhinus canicula* and *Carcharhinus perezi*; Jacoby et al. 2012). A network of white-striped freetail bat (*Tadarida australis*) roosting sites was found to have a communal roost which if

removed would seriously disrupt the network while the removal of any other site would have limited effects (Rhodes et al. 2006). In the only comparable prior study of a weighted network, the simulated targeted removal of honeybees with high strength from a network of food transfer interactions led to large decreases in the overall network connectivity (Naug 2008). Dolphin networks have also been shown to be more susceptible to targeted than random removals though relatively robust to both (Lusseau 2003, Lusseau and Newman 2004). Similarly, the chimpanzee networks studied here were not particularly susceptible to either targeted or random removals, but targeted removals did have a slightly stronger effect overall. Thus, vulnerability to targeted but not to random removals appears to be a common feature of many animal societies. The only current animal networks to have been studied that do not display this feature are the roosting networks of the leaf-roosting bat. Of three networks investigated, one was found to be highly susceptible to both targeted and random removals while the other two were robust to both forms of attack – although in both cases targeted removals still had a greater impact on network fragmentation than random removals (Chaverri 2010).

The results presented here are particularly interesting as they compare simulations performed on both binary and weighted networks. The results were largely similar for the two orangutan networks and the two chimpanzee networks, providing support for the validity of results obtained from binary networks, which by definition contain less information on the true structure of the network. However, for the orangutan networks the effects of targeted removals did appear to be more dramatic overall on the weighted network than the binary network, particularly in relation to weighted path length. This increased to a maximum of nine times the original value compared to less than three times the original value in the binary network. This may be a consequence of the difference between the two measures of path length, but certainly shows that there are

slight differences in the results depending on which method of network construction is employed. The analysis of weighted networks is therefore recommended, as this provides additional information about network vulnerability; however, if there is insufficient data or time to collect the data to create a weighted network, binary measures could still provide a valuable indication of the most appropriate targets for vaccination.

The vulnerability of the orangutan network to targeted but not random removals has a number of implications for disease transmission, both positive and negative. The negative consequence of such vulnerability is that the death of the key individuals in the network could have a considerable impact on network connectivity and cause the network to fragment (Lusseau 2003). This suggests that the introduction of a fatal disease into the orangutan population could have severe consequence for the cohesion of the community, at least temporarily. Although the network would likely rearrange in response to member deaths, this would clearly be a disruptive process for the population as in socially bonded species such as primates, the death of group members can have important impacts on both individuals and the overall social group (Engh et al. 2006, Barrett et al. 2012). The greater vulnerability to targeted removals suggests that this population of orangutans is particularly vulnerable to the loss of its most central members; the death of these individuals could cause the network to fragment. This is a worrying result as the most central group members are all resident adult females. These individuals may be more vulnerable to hunting pressure, as adult females, particularly if accompanied by an infant, are preferred targets for poachers (Mittermeier 1987). The high centrality of these females also means that they are more likely to contract disease and are consequently more likely to die in an epidemic. The death of these individuals could have serious negative impacts on the cohesion of the orangutans at Sabangau.

The positive implication of the vulnerability to targeted removals is that it provides further support for the argument that targeted vaccinations could be an extremely efficacious preventative measure in this population and perhaps in orangutans more generally. The removal of individuals from the population simultaneously removes all pathways that pass through these individuals. This simulates the vaccination of the removed individuals, as vaccination would prevent an individual from catching and spreading a disease, destroying all possible disease pathways that pass through the individual. The results of the simulations in this chapter show that the random vaccination of orangutans in this population would have very limited effects on preventing or slowing disease spread, while targeted vaccination would quickly reduce the number of possible pathways for disease transmission, thus limiting the size and speed of the resulting epidemic. It is also important to reiterate that the isolated individuals were removed from the above analyses as they will not be involved in disease transmission. However, the inclusion of these individuals would lead to an even lower impact of random vaccinations on average, as the random vaccination of the isolated individuals would evidently have no impact at all on disease dynamics.

Interestingly, resident females rather than transient individuals were highlighted as the best candidates for targeted vaccination as a result of their central positions in the network. As deforestation and the rise of ecotourism bring humans and orangutans into greater proximity, disease risk is likely to become a more important issue in orangutan conservation. Evidence indicates that targeted vaccination has been an effective means of preventing a widespread rabies epidemic in Ethiopian wolves (Haydon et al. 2006), suggesting that this may be a useful strategy for future disease prevention. Although it would be useful to compare the results obtained in the current study to those from a wider population of orangutans, the sample of orangutans studied here show clear signs

that targeted vaccinations could be a useful way of reducing the size and impact of future epidemics.

The chimpanzee community, in contrast, does not appear to be particularly vulnerable to either form of removal. This suggests that the death of individuals may have a lesser effect on cohesion than in the orangutan population. This is a result of the more even distribution of contacts in the chimpanzee community and consequently the high number of redundant links between individuals. Targeted removals had only a marginally greater impact on network connectivity than random removals, suggesting that the use of targeted vaccinations would not provide many additional benefits over simple random vaccinations. The relative robustness of the chimpanzee network to both forms of removals, however, implies that neither method would be particularly effective in this species. This has negative implications for the conservation of the chimpanzee as it suggests that any vaccination programme that focuses on only a select number of the community will have limited effects on reducing disease spread. A number of chimpanzee communities have already been recorded to suffer from respiratory epidemics, many of which were fatal, in addition to a devastating Ebola outbreak (Boesch 2008, Kaur and Singh 2008, Koendgen et al. 2008, Pusey et al. 2008). As deforestation and human encroachment continue and chimpanzee ecotourism gains popularity, the risks of disease transmission will increase and strategies to cope with disease will be necessary to reduce fatalities. The predicted failure of vaccination methods to reduce disease spread suggests that for chimpanzees the threat of disease must be combatted through preventative measures, such as the rules and regulations now commonly employed at ecotourism sites (Lukasik-Braum and Spelman 2008). The importance of these rules needs to be emphasised if widespread outbreaks are to be prevented among chimpanzees.

4.4.4 Limitations and future directions

There are a number of limitations to the analyses presented in this chapter that it is important to discuss. Firstly, the networks were based on the relationships observed between the apes in healthy populations that were not suffering from an epidemic. It is possible that the introduction of a disease would lead to changes in behaviour, altering the structure of the network (Craft and Caillaud 2011). The orangutan data were collected for only a small number of orangutans in a relatively limited geographical area (Morrogh-Bernard 2009). This means that the analyses cover only a small subset of the overall population of the Sabangau forest. This is particularly relevant in relation to the more migratory individuals, whose complete range of social relationships will not have been recorded, compared to the resident animals which were observed for longer and more consistently over the study period. Using a weighted network helps to reduce the impact of this problem, as association indices are standardised by observation time. In addition, the data were collected over a nine year period so it seems reasonable to assume that the large majority of relationships that are present between the animals within the network were recorded during this time period and therefore represented in the network. Ultimately, however, this problem results from the social organisation of the orangutan into very loose and fluid communities. In species in which community membership is more fixed such as the chimpanzee, this is clearly less of an issue. For the orangutan this issue would be difficult to completely resolve without the huge expense and effort that would be required to collect data on a wider population. It would be extremely interesting to be able to collect and analyse these data to explore orangutan networks at a broader level; nevertheless the results presented here provide a valuable first indication of the susceptibility of the orangutan network to disease. It is also important to note that these analyses are looking at the overall vulnerability of

chimpanzees and orangutans to disease in relation to particular features of their social organisation. Although in many disease studies it is recommended that short-term data are used to incorporate the dynamic nature of relationships, this study aimed to determine if general features of chimpanzee and orangutan social structure would facilitate or reduce disease spread. This sort of analysis benefits from long-term data, particularly for an elusive species such as the orangutan which requires large amounts of data to achieve an accurate impression of its social system.

4.5 Conclusion

The social structure of the orangutans at Sabangau suggests some vulnerability to infectious disease, although perhaps to a lesser degree than more social primate species such as chimpanzees. The death of the most central individuals from disease could have considerable ramifications for the cohesion of the orangutan population while chimpanzee networks appeared relatively robust against member death. Potential disease transmission should consequently be viewed as a threat to the conservation of both the orangutan and the chimpanzee that needs to be considered in all ecotourism and reintroduction initiatives. However, the risk to orangutans could possibly be reduced by the use of targeted vaccinations. The results suggest that such vaccinations could effectively destroy major disease transmission pathways and thereby help to prevent widespread epidemics. In contrast, targeted vaccinations would be less beneficial for the more social chimpanzee and so greater emphasis should be placed on alternative preventative measures.

5. The Spread of Infectious Disease across Orangutan and Chimpanzee Association Networks

5.1 Introduction

5.1.1 The threat of infectious disease

Infectious disease poses a serious risk to the future survival of great ape populations. Chimpanzees and gorillas, for example, have suffered from outbreaks of diseases such as Ebola (Bermejo et al. 2006, Boesch 2008), polio-like diseases and mange (Pusey et al. 2008), measles and scabies (Wallis and Lee 1999) and various unidentified respiratory diseases (Cranfield 2008, Kaur and Singh 2008, Koendgen et al. 2008, Pusey et al. 2008, Williams et al. 2008) and there is evidence that some of these infections may have been transmitted to the apes from humans (Kaur et al. 2008, Koendgen et al. 2008). Although no studies to date have described an epidemic among

orangutans, disease may still pose a major threat to these animals. In order to protect orangutans effectively from disease, it is important to gain an understanding of the way in which different types of disease could potentially spread within a population. This will provide an indication of the level of threat posed by different types of diseases, and the impact that they may have on the survival of the orangutan.

Currently, very little is known about the way in which disease would be expected to spread through orangutan populations; disease transmission within a wild orangutan population has not ever been recorded. Evidently, introducing a disease to wild orangutans in order to observe and record its spread is not an ethical possibility. Alternative methods therefore need to be used. Recently developed modelling approaches provide a means by which the impact of infectious disease on orangutans can be explored, by simulating the spread of disease within an orangutan population. This can be compared to the spread of disease in the more gregarious chimpanzee, to elucidate the effects of fine grained differences in social structure on predicted disease dynamics, while also providing useful information for the conservation of both species. In particular, simulating the spread of disease on a chimpanzee network may provide indications of the risk that disease poses to orangutans forced to live in closer proximity, such as those in rehabilitation centres and in forest fragments where densities are temporarily very high.

In order to provide more detailed insights into potential disease transmission in these species, there are a range of questions that need to be addressed. Firstly, it is vital that the general vulnerability of both orangutans (*P.p. wurmbii*) and chimpanzees (*P.t. schweinfurthii*) to disease transmission is assessed. This was investigated in the

previous chapter in relation to the way in which social network structure and the position of individuals within it impacted upon predicted disease spread. These analyses will be extended to provide a more in-depth understanding of susceptibility to disease by simulating the spread of disease on each network and measuring the magnitude of the resultant epidemic. Diseases with different properties, for example varying in the speed of transmission and recovery, will be simulated. This will demonstrate the predicted speed and extent of disease spread in both orangutans and chimpanzees under a range of disease scenarios, which will provide both an overall indication of the level of threat that disease poses to each species, as well as highlighting the types of diseases that may be particularly damaging. In addition to overall effects on population size, it is also important to explore the role of individuals in disease spread. The ability to spread disease and the probability of each individual becoming infected will be compared with individual measures of centrality to determine if central animals are indeed superspreaders. Finally, it is important for future conservation measures that the efficacy of different vaccination strategies in reducing disease spread and preventing epidemics is assessed. This was initially explored in Chapter 4, but will be investigated further by simulating vaccinations and measuring the effect on subsequent disease transmission. These analyses will contribute to the current literature on disease transmission in orangutans and chimpanzees, and in addition provide an assessment of the level of threat that disease poses to both ape species and the potential strategies that could be adopted to alleviate this threat.

5.1.2 Modelling the spread of disease

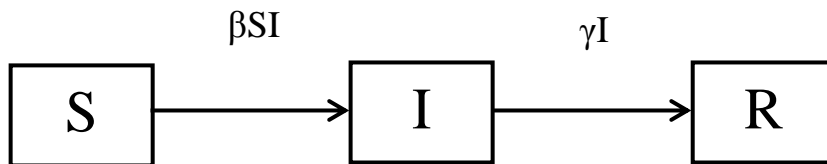
Modelling approaches provide a valuable method through which to investigate potential disease spread. Modelling the dynamics of disease transmission has a long history; the first attempt at mathematical modelling of disease dates back to a paper by Bernoulli (1760) on the use of inoculation in the prevention of smallpox (Isham 2004). The formulation of mathematical statements to describe infectious disease transmission, however, did not occur until the beginning of the 20th century (Kermack and McKendrick 1927, Anderson and May 1991). Hamer (1906) first suggested the principle of ‘mass-action’, which states that the number of new infections (and thus the course of an epidemic) is a product of the number of infected individuals and the number of susceptible individuals (Anderson and May 1991, Grassly and Fraser 2006). This principle is based on the assumption that the rate of contact between susceptible and infected individuals is constant throughout the population, which has since been termed homogenous mixing (Moreno et al. 2002). Kermack and McKendrick (1927) created a simple mathematical model of the way in which disease would be expected to spread in such a homogeneously mixed population over time. Their basic compartmental model describes a population composed of susceptible (S), infected (I) and recovered with immunity (R) individuals (Kermack and McKendrick 1927). The model is deterministic, meaning that it will always predict exactly the same outcome from given starting conditions; chance events are not included (Dangerfield et al. 2009). Births and natural deaths (i.e. not disease related) are also not included as the time-scale of the disease is assumed to be much shorter than the lifespan of the individuals in the population (Moreno et al. 2002). The model is described by three differential equations:

$$\frac{dS}{dt} = -\beta SI$$

$$\frac{dI}{dt} = \beta SI - \gamma I$$

$$\frac{dR}{dt} = \gamma I$$

Such that:



Where S is the number of susceptible individuals in the population, I the number infected and R the number recovered. These variables are not restricted to integer numbers and it is not possible to track the disease status of particular individuals (Isham 2004). β is the transmission coefficient (the rate at which disease is transmitted between susceptible and infected individuals) and γ is the recovery rate (the rate at which individuals recover). As many infectious diseases confer lifelong immunity, in most models recovered individuals remain in this state and do not revert back to susceptible status (Anderson and May 1991).

As described above, this deterministic mathematical model always produces the same predictions of the number of individuals in each category given the same initial conditions. This is not an accurate representation of reality as stochastic factors can play an important role in epidemic dynamics. This is particularly true in small populations and when a disease begins to decline in prevalence, when stochastic events can become

extremely influential in determining if a disease will become extinct or regenerate (Isham 2004). The extinction of an epidemic disease as a result of random fluctuations in the number of susceptible and infected individuals is termed epidemic fade out (Lloyd-Smith et al. 2005). Stochasticity can be incorporated into models of disease spread by replacing the rate of change from one state to another in the deterministic model with the probability of a change in state (Cassels et al. 2008). Some of the earliest stochastic disease models include those of McKendrick (1926) and the chain binomial model of Reed and Frost proposed in a series of lectures in 1928 (Wilson and Burke 1942, Wilson and Burke 1943, Daley and Gani 2001). These models were also based on the assumption of homogenous mixing.

Disease modelling has continued to develop since these early advances and there are now a number of variations on the compartmental Susceptible-Infected-Recovered model (SIR model). Different classes of infection status can be included; for example, the Susceptible-Infected model describes a disease from which individuals do not recover and so a recovered state is not necessary (Bai et al. 2007). Diseases which do not confer any immunity can be modelled using a Susceptible-Infected-Susceptible model, in which infected individuals always revert back to susceptible status (Eames and Keeling 2002). If a disease confers a short period of immunity this too can be modelled, by including a recovered state, followed by a reversion to susceptibility in a Susceptible-Infected-Recovered-Susceptible model (Grassly and Fraser 2008). A latent period, during which an individual is infected but not yet infectious, can be incorporated into the model with the inclusion of an exposed state in a Susceptible-Exposed-Infected-Recovered model (Drewe et al. 2011). Further complexity can be added to these models

with the inclusion of demographic parameters such as birth and natural death rates or preventative measures such as vaccinations (Bai et al. 2007, Rizkalla et al. 2007).

Homogeneous mixing models, both deterministic and stochastic, have been used to provide useful insights into many different diseases, particularly in humans (Anderson and May 1991). The dynamics of various infectious diseases that affect humans have been explored, such as HIV (Anderson et al. 1986, Anderson et al. 1988) and varicella (Giraldo and Palacio 2008). Studies are not restricted to humans, however, as the models have also been applied to a number of non-human animal species. A model of myxomatosis in rabbits (*Oryctolagus cuniculus*) that included demographic parameters predicted that for all realistic values of these parameters the virus would control the size of the rabbit population (Dwyer et al. 1990). Fulford et al. (2011) modelled simultaneous outbreaks of myxomatosis and rabbit calicivirus disease (RCD) and found that the introduction of RCD may suppress myxomatosis prevalence. These models have also been used to investigate epidemics in livestock; for example, a model of foot-and-mouth disease in the UK compared a simulation in which varying proportions of animals were culled to one in which they were vaccinated. The model predicted that culling was a much more effective preventative strategy than vaccination once an outbreak has begun, as even high rates of vaccination failed to prevent widespread deaths (Wood 2007). This approach has also been applied to primates; for example, the spread of Ebola between gorillas has been investigated (Rizkalla et al. 2007). This involved the creation of an SIR model that assumed homogenous mixing and included births, natural deaths, deaths resulting from Ebola and a hunting rate. This model predicted an 80% decline in gorilla numbers in 39-43 years and a 97% decline in 100 years (Rizkalla et al. 2007).

Despite the evident utility of these models, they have been criticised on the basis that the assumption of homogeneous mixing is a considerable simplification of reality (Sattenspiel 1990, Getz et al. 2006, Bansal et al. 2007). Instead it is likely that individuals vary in their contact patterns and are far more likely to come into contact with their close associates than with random individuals in the population. These heterogeneous contact patterns are likely to have a strong effect on the way in which disease spreads within the population (Moreno et al. 2002). Incorporating heterogeneity in mixing patterns is likely to be critical to a more complete understanding of disease dynamics. One method of increasing heterogeneity in mixing patterns is to include different classes of individuals into an SIR model, based on age or sex. Different age classes may differ in their levels of sociability, which could impact their chances of becoming infected or spreading disease. Contact rates among adult wild boar (*Sus scrofa*), for example, are higher than among juveniles (Bolzoni et al. 2007). This difference was incorporated into an SIR model of Classical Swine Fever by including two age classes that varied in transmission rate. Importantly, this model suggested that disease prevalence actually increased with culling rate and peaked at intermediate levels of culling. Only very high levels of culling were predicted to reduce disease prevalence. This indicates that failing to recognise these heterogeneities in contact patterns could lead to the implementation of ineffective culling strategies (Bolzoni et al. 2007). Similarly, age classes that differed in transmission rate were included in a Susceptible-Exposed-Infected model of devil facial tumour disease in the Tasmanian devil, which also predicted that a very high rate of culling would be necessary to prevent host extinction from disease, and therefore that culling was not a viable preventative strategy (Beeton and McCallum 2011).

5.1.3 Incorporating heterogeneity in contact patterns into epidemiological models: network models

Consideration of the impact of variation in susceptibility between different age/sex classes can evidently provide a more accurate approximation of disease spread. However, individuals within these classes may also vary in their contact patterns, and so this is still not an entirely accurate representation of disease spread within a population. This is particularly relevant when investigating at the level of a social group, in which individual variation in behaviour will have a very important impact on disease spread. Consequently, models have been developed that simulate the spread of disease across social networks, where individuals vary in their social tendencies. Disease spreads from infected to susceptible individuals within the network with a probability that is equal to the product of the transmission coefficient and the association index of the dyad (Cross et al. 2004). In this way, the spread of disease is dependent on the presence and strength of actual relationships between individuals. In addition, these models are individual-based, which means that the infection status of specific individuals in the population can be determined, and stochastic, so the impact of random events on disease spread is included in the model predictions. Although computationally and data intense, creating a model using a network based on data of observed patterns of behaviour seems important to gain a more reliable model of disease spread in a group. Indeed, predictions obtained from a simulation of the spread of influenza on a network based on close contacts between people in a school were shown to closely match observed data on absentees during an influenza season (Salathé et al. 2010), providing strong support for the value of this approach.

It has been demonstrated for a range of network structures that the topology of the network has a great influence on the spread of disease; for example, diseases have been shown to spread extremely quickly through scale-free networks (Pastor-Satorras and Vespignani 2001, Moreno et al. 2002). Keeling (2005) simulated the spread of disease on a range of networks varying in clustering and found that higher levels of clustering led to reduced disease transmission. Networks varying in community modularity (i.e. the extent to which a network is divided into subgroups) have also been shown to vary in predicted disease dynamics; higher community modularity led to greater variation in the size and duration of the predicted epidemics and led to a higher number of small, local outbreaks (Salathé and Jones 2010). Similarly, Griffin and Nunn (2012) simulated the spread of disease across theoretical social networks that varied in community modularity. They found that increased community modularity led to reduced disease spread. The community modularity in social networks from 19 primate species was then compared with parasite richness in these species and it was shown that increased community modularity was indeed associated with a lower richness of socially transmitted parasites (Griffin and Nunn 2012). These results highlight the importance of social network structure for disease transmission.

In this chapter, a network SIR model will be created in order to investigate the spread of disease within an orangutan (*P.p. wurmbii*) population and a chimpanzee (*P.t. schweinfurthii*) community. Network models often produce very different results from those obtained using homogenous mixing models. An SEIR model of a network of cattle movements in the UK, for example, predicted that disease spreads less in the network than would be predicted using a mean-field (homogenous mixing) model (Duncan et al. 2012). Mean-field models also produced consistently higher estimates of

the level of infection with sexually transmitted diseases in humans (Eames and Keeling 2002) and tuberculosis in buffalo (*Syncerus caffer*; Cross et al. 2004) compared to network models. The spread of disease across the orangutan and chimpanzee networks will be compared to that on networks of the same size in which individuals are assumed to mix homogenously and networks in which individuals mix randomly, to explore the impact of incorporating the actual topology of the network on model predictions. Network analyses of disease transmission in orangutans and chimpanzees have not previously been performed using SIR models.

Infectious diseases differ considerably in their relative infectiousness and the length of the infectious period; for example, tuberculosis has a relatively low infectiousness but very long periods until recovery (Baxter 1993, WHO 2013). In contrast, diseases such as Ebola, influenza and measles are extremely infectious and infected hosts die or recover more rapidly (Chowell et al. 2004, Rizkalla et al. 2007, WHO 2013). Diseases like Hepatitis B may lead to chronic infections that last for extended periods, during which the carriers can remain highly infectious (WHO 2013). There is clearly a broad range of diseases that vary in both their absolute and relative transmission and recovery parameters. One of the main applications of network models is to assess vulnerability to disease, including diseases that differ in their transmission and recovery properties, in terms of the proportion of individuals that become infected. A disease with equivalent transmission and recovery probabilities was simulated on a weighted killer whale network and found to spread rapidly to 90% of the community, indicating extreme vulnerability to disease outbreaks (Guimarães et al. 2007). Cross et al. (2004) investigated disease transmission in buffalo weighted association networks and found that disease spread more extensively during dry conditions as a result of greater

clustering in the network compared to wet conditions. This study also compared the spread of diseases with low infectiousness and slow recovery to the spread of those with high infectiousness and rapid recovery. Diseases with low infectiousness and slow recovery were found to be more likely to persist, which led to increased opportunities for disease transmission between herds and hence the infection of a greater number of buffalo overall (Cross et al. 2004).

Although the exact disease parameters for any of these diseases are not known for orangutans and chimpanzees, it is possible to vary transmission and recovery coefficients in simulations to provide an indication of the susceptibility to different general types of infectious disease. Again this will be compared to a mean-field network (but not to random networks due to computational constraints) to highlight the importance of incorporating heterogeneous mixing patterns. Comparing the results for an orangutan network with those from chimpanzees will provide an indication of the different levels of threat faced by the two species and how this is affected by differences in social structure. Individually, the models should provide a degree of advanced warning as to the impact that different types of diseases may be expected to have on each species. This could be valuable for the design of strategies to both prevent and respond to disease spread in these species.

It is also important to investigate more specific features of disease transmission, such as the role of particular individuals in spreading disease. An SEIR model to explore the spread of tuberculosis across meerkat grooming and aggression networks, for example, showed that groomers were at a higher risk of tuberculosis infection than groomees, and that grooming was more likely than aggression to be associated with transmission

(Drewe et al. 2011). High centrality in a network has been found to be associated with an increased risk of infection (Corner et al. 2003, Drewe 2010) and may also be associated with an increased ability to spread disease (Woolhouse et al. 1997). Individuals with particularly high centrality relative to the other members of the network have been identified in the orangutan network, but not the chimpanzee network (Chapter 4). It was inferred that these individuals may play a more important role in disease spread amongst orangutans, and may also be more likely to become infected; these individuals were termed potential superspreaders. In this chapter, the validity of this suggestion will be explored using SIR models. If highly central individuals are indeed more important in disease dynamics, there should be a clear relationship between their centrality and both the number of secondary cases that they cause and the number of times that they become infected (Christley et al. 2005, Eames et al. 2009). This will provide further insights into the importance of high centrality for both spreading disease and becoming infected.

Finally, it is important to explore the impact of vaccinating central individuals on overall disease spread, and again this can be assessed using network epidemiological models. The effect of simulated targeted vaccinations can be compared against random vaccinations to determine the relative efficacy of each method in reducing disease spread. Targeted vaccinations of the most central individuals have been shown to be more effective in reducing epidemic size in scale-free and small-world networks (Pastor-Satorras and Vespignani 2002, Zanette and Kuperman 2002, Bai et al. 2007) and a network of human physical contacts (Eames et al. 2009). Results in Chapter 4 have already shown that the orangutan network but not the chimpanzee network was susceptible to the targeted removal of central animals, indicating that targeted

vaccinations may be a useful disease prevention strategy. Incorporating vaccinations into the SIR models is a valuable method of investigating this in more detail.

5.1.4 Static and dynamic network models

Network models can either be based on static or dynamic networks. Static simulations focus on one network, with all edges representing the strength of the relationship between two individuals over the whole study period. In contrast, dynamic networks include temporal changes in contact patterns, i.e. networks are updated with each time step (Danon et al. 2011). A static SIR model assumes that the probability of disease spreading from one individual to another is proportional to the amount of time two animals have spent together over the entire data collection period. This is assumed to provide an accurate approximation of the general patterns of relationships between individuals in the network and hence of the overall social organisation. A model run on a static network is therefore assumed to provide an indication of the way in which disease would be expected to spread on average, based on the overall structure of the society. This may be misleading as it fails to account for short-term relationships that change as a result of ecology or demography, which will have an important effect on the pattern of disease transmission. Therefore, it may be more useful to analyse a dynamic network, in which relationships vary over shorter periods of time (Cross et al. 2009).

For dynamic network models, networks are based on shorter sampling periods, for example, two years of observation data of buffalo were separated into monthly networks (Cross et al. 2004). The simulation model is then performed using time steps equivalent to the sampling period. At each time step, disease spreads within the network in accordance to the contact patterns during that particular time. This provides a more

accurate picture of the way in which disease would spread in a social group, unless contacts change at a rate far slower than the rate of disease spread (Volz and Meyers 2007). To date, most network models have been static, as a result of the lack of the in-depth data required for dynamic models (Cross et al. 2009). However, dynamic models can produce different results to static models (Vernon and Keeling 2009). It can be argued that dynamic models are based on more realistic data and so the predictions are more likely to represent reality. If this argument is correct, differences between predictions from static and dynamic models may suggest that static models are not an adequate approximation of disease spread (Volz and Meyers 2009, Grabowski and Rosińska 2012).

The individual networks that make up a dynamic model can also be investigated in turn, to explore the extent to which disease spreads when only one month of data is considered and how this varies between months in different seasons. Diseases were predicted to spread more between buffalo during dry conditions than wet conditions (Cross et al. 2004), for example, indicating that the season can have an important effect on disease spread.

The resolution of the orangutan data was not high enough to allow for the simulation of a dynamic model; only the total time that each dyad spent in association over the nine years was available. However, the composition of chimpanzee parties during all focal scans that took place over the three years of data collection was available and so a dynamic model could be created based on monthly networks. Creating both static and dynamic network models for this species will illuminate the importance of incorporating dynamism into the chimpanzee model as well as giving a more in-depth insight into

potential disease spread within chimpanzees. However, investigating disease spread for the orangutan at a higher temporal resolution than the static model requires a different approach.

5.1.5 An alternative dynamic model: agent based modelling

An alternative method of modelling disease transmission that is considerably less data intensive is agent based modelling. Agent based models are simulation models in which individuals are autonomous agents that interact with each other and their environment (Railsback and Grimm 2011). This method involves the creation of a state space representing the environment, and agents that represent individuals. The agents are given set rules which govern their behaviour, such as their patterns of movement throughout the state space, or their social interactions with other agents. In this way, both the overall system that emerges and the behaviour of individuals within the system can be explored (Grimm et al. 2006).

An important benefit of agent based models is that they can incorporate the influence of spatial proximity on association patterns (Kramer-Schadt et al. 2009). This is achieved by separating the state space into habitat patches and allocating particular habitat patches or territories made up of a number of patches to specific agents (Kramer-Schadt et al. 2009). Individuals can disperse from these patches with a given probability and contact only those other individuals that are within a certain distance of their habitat patch (Salkeld et al. 2010). Differences between individuals in sociality or ranging behaviour can also be included in these models by varying the dispersal distances and probabilities of contact between age/sex classes or even between individual agents

(Railsback and Grimm 2011). Thus, agent based models are another method through which dynamic, heterogeneous social relationships can be modelled.

The spread of disease can be simulated between individuals in an agent based model using the SIR framework. Consequently, agent based modelling can provide valuable insights into potential disease spread at a high temporal resolution. An agent based model of red colobus monkeys, for example, showed that the distribution of resources in logged forests may lead to increased rates of disease transmission between groups of monkeys compared to unlogged forests (Bonnell et al. 2010). An agent based model of Classical Swine Fever in wild boar predicted that disease tended to persist in the youngest age class and that vaccinations may not be an effective preventative strategy (Kramer-Schadt et al. 2009). An agent based model of the spread of rabies in a general host resembling a small canid predicted that the non-uniform spreading of vaccination may be more effective in some cases than the uniform spread commonly employed (Bohrer et al. 2002). These models can also be used to look at inter-specific disease transmission. For example, a model of prairie dogs (*Cynomys ludovicianus*) and grasshopper mice (*Onychomys leucogaster*) predicted that the presence of these mice would exacerbate the spread of plague through the dog coterie (Salkeld et al. 2010).

Nunn et al. (2008) created an agent based SEIR model to investigate the effect of varying social and infection parameters on the resulting disease transmission in chimpanzees and gorillas. The size and composition of groups of apes were randomly generated (within certain constraints), a dispersal probability for each individual at each time step (one day) was set and disease was introduced to one female in the population. Dispersal probabilities were sex specific and individuals always dispersed if the number

of the opposite sex within the group fell below a certain threshold. Mixing within social groups was homogenous and disease was assumed to only spread within groups (i.e. individuals within a group could only become infected if an infected individual joined the group, disease could not spread during encounters between groups). The spread of disease within the population was then simulated. Each of the parameters was varied and the simulations repeated to determine if this led to a change in the disease dynamics.

Simulations of single-male groups, groups with higher rates of dispersal and a greater number of females in the groups as well as those of diseases with longer incubation periods were all associated with greater disease spread. The model was then run using actual group composition data from chimpanzee and gorilla populations and estimated disease parameters for Ebola. These simulations showed that overall more individual chimpanzees became infected than gorillas, but that disease spread to a greater number of gorilla groups. This is likely to be a result of their differing social systems; chimpanzees live in larger groups, so disease can spread to more individuals within groups, while gorillas often live in single-male groups and once the male has died of Ebola, the females will disperse to other groups potentially carrying the Ebola virus with them (Nunn et al. 2008). This model provided a lot of novel information about the potential spread of disease within apes. It showed clearly the effect that differences in social structure can have on disease spread as well as highlighting the vulnerability of both chimpanzees and gorillas to disease.

Agent based models evidently provide a valuable method of investigating disease transmission at a higher temporal resolution than can be achieved using static network

models. An agent based model was therefore created for the orangutan to determine if this higher temporal resolution leads to different predictions of disease spread than those produced using the static network model. An SIR model can be incorporated and diseases simulated with varying transmission coefficients and probabilities of recovery, to explore the way in which different types of diseases spread between orangutans. This can be compared to the results using the static network model to highlight the importance of investigating disease over short time frames in this species as well as providing additional evidence regarding potential disease spread between orangutans.

5.1.6 Chapter aims

1. To determine the importance of using actual network data to investigate disease transmission. This will be achieved by comparing predicted disease spread across the association network with the results obtained using random and mean-field networks (i.e. networks in which individuals mix homogenously) for both orangutans and chimpanzees.
2. To predict the extent to which diseases with different transmission and recovery parameters spread in the orangutan and chimpanzee networks.
3. To investigate the effect of high centrality in both orangutan and chimpanzee networks on both the probability of becoming infected and the ability of individuals to spread disease.
4. To assess how random and targeted vaccinations could reduce disease spread in both orangutan and chimpanzee networks.

5. To determine if short-term variation in social behaviour impacts upon disease predictions for chimpanzees, by comparing results from a chimpanzee dynamic model to those from the static model.
6. To investigate the predicted spread of disease over a one month time period in the chimpanzee network and determine whether or not this varies by season.
7. To determine if short-term variation in social behaviour impacts upon predicted disease spread in orangutans, by investigating the spread of disease between orangutans using an agent based model.

5.2 Methods

5.2.1 The static orangutan and chimpanzee SIR models

5.2.1.1 The effect of network topology on predicted disease spread

A stochastic individual-based discrete-time SIR model was created and used to model the spread of disease across both the orangutan and the chimpanzee association networks. The weighted networks described in the previous chapter were used, with weights representing the association index between two individuals. All individuals in the population start the simulations as susceptible, except for one randomly selected individual classed as infected. At each time-step disease spreads along the edges connected to the infected individual with a probability equal to the product of the association index and the transmission coefficient. Infected individuals recover at each time step with a probability equal to the recovery coefficient. The transmission and recovery coefficients were both set at 1.0 for the first model run on both the orangutan and chimpanzee networks. This means that disease spreads between an infected and a

susceptible individual with probability equal to the association index, and infected individuals recover in one time step. It is important to note that diseases varying in virulence will not be simulated and that for the purposes of the model, recovered individuals are equivalent to dead individuals. In both cases the individual is removed from the network and can no longer transmit the disease (as an individual that has recovered is assumed to be completely immune to further infection). In terms of the model it is consequently not important to specify the number that recover and the number that die. Evidently, biologically these states are not equivalent and the number of individuals that die or recover will depend on the disease. The proportion of individuals that die and recover can easily be estimated based on the results of the model and what is known about the disease. If a disease kills an average of 99% of those infected, the number of dead individuals is simply 99% of those in the recovered category.

The model was run for ten time steps on both networks. Ten time steps was chosen as this was sufficient for the disease to fade out in all simulations and so the complete pattern of disease spread could be analysed. This simulation was repeated 10,000 times and the mean number of individuals that were infected and recovered at each time step over the 10,000 simulations plotted. All SIR models were run using *tnet* (Opsahl 2009) in R (R Development Core Team 2011). The results of these simulations were compared with those from a mean-field network and with those from random networks, to determine the importance of incorporating heterogeneity for disease dynamics. The mean-field network was one in which all individuals were connected to all others i.e. the population was homogenously mixed. Each dyad associated with an association index that was equivalent to the mean of the association indices in the actual network. This

ensures that the overall force of infection in the mean-field network is the same as that in the actual network (Cross et al. 2004). The random networks were created using the links randomisation method using *tnet* (Opsahl 2009) in R (R Development Core Team 2011), whereby all of the edges in the network are reshuffled with their associated weights (Opsahl et al. 2008). The network was randomised 1,000 times and the SIR model simulated on each of the random networks 10,000 times. The number of individuals that were infected and recovered at each time step was averaged over the simulations for both the mean-field and the random networks and the results plotted for comparison with the original network results. This process was performed on both the orangutan and the chimpanzee network.

5.2.1.2 The spread of diseases with varying probabilities of transmission and recovery

In order to investigate the way in which diseases varying in their relative infectiousness and time to recovery would spread across the orangutan and the chimpanzee networks, the spread of diseases with different parameters was simulated. The transmission coefficient (β) and the probability of recovery (γ) were varied from 0.1 to 1.0 at intervals of 0.1 and diseases with all 100 combinations of values simulated (i.e. 0.1 and 0.1, 0.1 and 0.2, 0.1 and 0.3 etc). The SIR model was run 10,000 times on both the orangutan and the chimpanzee networks with all combinations of these parameters, to explore the way in which transmission and recovery probabilities impact disease risk. The final size of the epidemic was measured at the end of each simulation (once the disease had died out or all individuals had become infected and recovered). The final size of the epidemic is the total number of individuals that become infected over the course of the epidemic. In order to ensure that the disease had completely died out in all

simulations, the model was run with 1,000 time steps. The final size of the epidemic was compared between the different simulations as an indication of the susceptibility of the ape populations to diseases with varying parameters. This analysis was also performed on the mean-field network to investigate the influence of heterogeneous contact patterns under different disease parameters. Computational constraints meant that this could not be performed for the random networks.

5.2.1.3 The effect of individual network centrality on both the ability to transmit disease and individual infection risk

The relationships between measures of centrality and both the ability to spread disease and the probability of becoming infected were investigated for the orangutan and the chimpanzee networks. The ability of a specific individual to spread disease was quantified by selecting that individual as patient zero and running the simulation 10,000 times. The mean number of secondary infections (i.e. the number of individuals that became infected, excluding patient zero) was calculated. This analysis was performed for all individuals in the network. The mean number of secondary infections caused by each individual was then plotted against four binary measures of centrality (degree, betweenness, closeness and eigenvector centrality) and four weighted measures of centrality (strength, weighted betweenness, weighted closeness and weighted eigenvector centrality). Curve estimation procedures were used to determine the best equations (i.e. highest R^2 and significant p-value) to describe the shape of these relationships mathematically. This was performed on both the orangutan and the chimpanzee networks. For the orangutan network, the spread of two diseases was simulated, one with parameters $\beta=1.0$ and $\gamma=1.0$, which caused limited disease spread,

and one with parameters $\beta=1.0$ and $\gamma=0.1$, which caused much greater disease spread. This is to ensure that the conclusions drawn from the analysis are a result of the importance of individuals in the network and not the specific disease parameters chosen. These two combinations of parameters were chosen specifically as they lead to very different patterns of disease spread. Three diseases with differing parameters were investigated in the chimpanzee network; the first with parameters $\beta=1.0$ and $\gamma=1.0$, the second with parameters $\beta=0.1$ and $\gamma=0.4$ and the third with parameters $\beta=0.1$ and $\gamma=0.9$. The first of these diseases infects around 90% of the population, the second around 50% and the third around 20% and so they should give a reasonable representation of the effect of different types of disease. The range of disease parameters investigated differed from those looked at for the orangutan as the two populations respond to disease in very different ways. Simulating the spread of a disease with transmission coefficient 1.0 and recovery coefficient 0.1 on the chimpanzee network (as on the orangutan network) produces results that are very similar to those of the disease with transmission and recovery coefficients of 1.0. Therefore, although the comparison of these two diseases is appropriate for the orangutan, for the chimpanzee, the difference between the two is minor and so the comparison is not informative. Similarly, simulating the spread of diseases with parameters $\beta=0.1$ and $\gamma=0.4$ or $\beta=0.1$ and $\gamma=0.9$ on the orangutan network does not provide an interesting comparison as all diseases with low transmission coefficients struggle to spread on this network. As the purpose of this comparison is to test whether diseases varying in these key parameters share a similar relationship with centrality within networks, it does not matter that diseases differ between networks.

To explore the effect of centrality on the risk of infection, the number of times that each individual became infected over 10,000 simulations was calculated (in these simulations patient zero was selected at random). Infection risk is then defined as the percentage of simulations in which an individual became infected. This was plotted against the four binary and the four weighted measures of centrality to look at the relationship between centrality and infection risk. Again, this was repeated using two different simulated diseases for the orangutan ($\beta=1.0$, $\gamma=1.0$ and $\beta=1.0$, $\gamma=0.1$) and three for the chimpanzee network ($\beta=1.0$, $\gamma=1.0$; $\beta=0.1$, $\gamma=0.4$ and $\beta=0.1$ and $\gamma=0.9$).

5.2.1.4 The value of different vaccination strategies in reducing disease spread

The effect that different vaccination strategies would have on the overall size of the epidemic was assessed. Random vaccinations were simulated, as well as targeted vaccinations of individuals with high degree, betweenness, closeness, eigenvector centrality, strength, weighted betweenness, weighted closeness and weighted eigenvector centrality. Random vaccinations involved the stepwise vaccination of individuals selected at random from the network. Targeted vaccinations involved the stepwise selection of individuals with the highest score for each network metric. The models were run by first selecting the individual(s) to be vaccinated and assigning them recovered status. This means that they cannot become infected or transmit disease within the network, simulating vaccination. Patient zero was then randomly selected from the remaining individuals and the simulation run until the disease had died out, at which point the final size of the epidemic was calculated. This procedure was repeated for all vaccination strategies 10,000 times and the average results plotted for

comparison. This analysis was performed on both the orangutan and the chimpanzee static networks.

5.2.2 The importance of short-term relationships: the chimpanzee dynamic model

The creation of a dynamic network model was not possible for the orangutan, but the chimpanzee data were available at a high enough resolution to allow for the creation of monthly networks. Association indices were calculated on a month by month basis, and a separate network built for each month of the study period. Before running the dynamic model it was necessary to investigate if all of the monthly networks provided enough detail to represent the contacts that occurred within one month. The number of individuals and edges present in each monthly network and the number of 15 minute focal scans per month were therefore calculated for each of the networks.

The number of individuals and the number of relationships (edges) observed during each of the one month time periods are displayed in Table 5.1, along with the total number of 15 minute focal scans performed. It is clear that for the first six months the number of individuals observed and the number of edges were considerably lower than for subsequent months, which may result from lower observation effort during this time period, indicated by the low number of focal scans performed. However, for the remaining 30 months the number of individuals and edges is higher. The number of focal scans performed is also much higher in the last 30 months than the first six months. This suggests that over each of these 30 months there should be sufficient data on which to base a network; the lowest value is still over 124 hours of observation time in a month, while the highest is over 375 hours. This suggests that the monthly networks

from month seven onwards should be sufficient to depict realistic networks of chimpanzee social relationships.

Table 5.1: The number of individuals observed, edges in the network and focal scans performed for the chimpanzees, for each of the months of data collection.

Month	Number of individuals in network (out of 55)	Number of edges in network	Number of focal scans performed
1	26	182	176
2	29	248	223
3	29	141	287
4	35	406	221
5	39	590	277
6	39	567	189
7	42	796	551
8	40	727	1009
9	41	634	1200
10	39	713	1482
11	41	795	1015
12	41	715	496
13	40	656	719
14	43	633	969
15	41	659	1178
16	42	776	1349
17	41	735	590
18	41	745	798
19	45	826	863
20	40	682	1148
21	43	705	953
22	40	507	1394
23	36	439	1032
24	40	557	1153
25	39	651	1106
26	44	772	1333
27	41	778	1180
28	41	804	1390
29	41	663	784
30	42	817	961
31	41	687	1101
32	41	664	1295
33	41	692	1366
34	40	625	1503
35	43	651	1356
36	41	585	1495

The dynamic chimpanzee SIR model was therefore run using networks constructed from one month observation periods and run over the 30 months with sufficient data. One individual in the population was initially infected. This individual was constrained to be one of the individuals present in the first monthly network. 13 individuals were not present in the first monthly network and so could not be selected as patient zero as their social relationships during this period are unknown, meaning that disease spread from these individuals cannot be modelled. This is because individuals recovered from the disease within one time step and so if patient zero was not present in the first network, disease would not spread at all. This would lead to an underestimation of average disease spread.

At each time step disease could only spread from infected individuals to their contacts that occurred during that time step. The time step was set at one month, so at each time step a new network was used to calculate the probability of infection, i.e. for time step one, the first month of data was used, for time step two, the second month etc. The simulation had a total of 30 time steps. Infection spread across edges with a probability equal to the product of the transmission coefficient and the association index for that time step (i.e. the association index for the relevant monthly network). As in the original static models the transmission coefficient was set at 1.0. Individuals recovered with a fixed probability at each time step, again set at 1.0 for the first run of the model. The numbers of individuals that were infected and recovered at each time step were calculated. These were compared against the number of infected and recovered individuals at each time step for a static model based on the same 30 months of data.

To investigate the effect of different types of diseases on the dynamic model, the transmission and recovery coefficients were then varied from 0.1 to 1.0 at intervals of 0.1 and a model with every combination of parameters run. The model was restricted to 30 time steps, and so for low recovery rates, the disease may not have died out by the end of the simulation. As it is not possible to continue the dynamic simulation beyond 30 time steps (as there are only 30 months of data), it is consequently not possible to calculate the final size of the epidemic. Instead, the number of recovered individuals after 30 time steps is measured, which is likely to be slightly less than the actual final size of the epidemic in some cases. This procedure was repeated on the static network based on the same 30 months of data to determine if the two methods produced similar results.

5.2.3 Diseases that spread over a shorter time frame: chimpanzee monthly networks

The spread of a disease with a transmission and a recovery coefficient of 1.0 was simulated 10,000 times across each of the 30 monthly networks in turn for ten time steps. The number of individuals infected and recovered at each time step was calculated for each network and the results averaged, to provide a prediction of the way in which disease would be expected to spread on average over a one month time period. The average final size of the epidemic was calculated for each of the networks. To determine if observation effort affected the predictions, the relationship between the final size of the epidemic for each month and the number of focal observations performed during that month was investigated using Pearson's correlation in SPSS (SPSS 2008). In addition, the degree of similarity between each of the monthly networks and the overall network based on all 30 months of data was assessed. This was

achieved using the quadratic assignment procedure in UCINET (Borgatti et al. 2002). This computes Pearson's correlation coefficient between corresponding cells in two matrices. The rows and columns in one of the matrices are then randomly permuted, in this case 50,000 times, and the correlation recalculated to give a distribution of correlations based on randomised networks (Hanneman and Riddle 2005). The original correlation can be compared against this distribution of values to determine if it is significantly different from random (Borgatti et al. 2002).

The networks were then separated into those collected during months in the dry season and those collected during the rest of the year to determine if there was an effect of season on disease dynamics. In Budongo, rainfall is fairly heavy and predictable throughout most of the year, the exception being the dry season from the beginning of December to the beginning of March (Newton-Fisher 1997). The networks from December, January and February were therefore classed as the dry season and those from the rest of the year classed as the wet season. Predicted disease spread during these two seasons was compared using a Mann-Whitney U test in SPSS (SPSS 2008).

5.2.4 The importance of short-term relationships: the agent based model for the orangutan

The agent based model was built in Netlogo (Wilensky 1999). The model will be briefly described using the ODD (Overview, Design concepts and Details) protocol (Grimm et al. 2006; see Appendix G for full model description including estimation of parameters, and for details of model testing).

5.2.4.1 State variables

There are 46 agents in the model, each representing an orangutan. Each agent has both an age/sex class (adult female, adolescent female, unflanged male or flanged male) and a residential status (resident, regular visitor, occasional visitor, rare visitor or very rare visitor), based on the demography of the population at Sabangau (Morrogh-Bernard 2009). Individuals also have (i) home ranges, which they do not leave - 314 hectares for flanged males, 254 hectares for unflanged males and 227 hectares for females, (ii) a probability of being present in the area – residents are present 75% of the time, regular visitors 38%, occasional visitors 15% and rare and very rare visitors 4% (Morrogh-Bernard 2009), and (iii) an epidemiological status – susceptible, infected or recovered. The state space is composed of patches representing areas 50m by 50m, with the whole space making up the 900 hectare study area at Sabangau (Morrogh-Bernard 2009). At Sabangau 47% of trees were classed as potential orangutan feeding trees, and so 47% of patches are set as potential feeding sites, of which during each month between 2-9% are in fruit, 20-50% in leaf and 2-11% in flower (Morrogh-Bernard 2009). These patches are allocated a value for energy content in proportion to the percentage of time that orangutans at Sabangau spend eating these three types of food (fruit between 800 and 3600, flowering between 200 and 800 and leafing between 150 and 200 energy points). A time step represents half an hour.

5.2.4.2 Process overview and scheduling

Each month (i.e. 720 time steps – see 5.2.4.4 below) individuals appear in the area with the probability associated with their residential class. Each month the percentage of patches in fruit/flower/leaf changes and the patches are updated accordingly and every

two days, if the resources on a patch that is in fruit/flower/leaf are depleted, the patch regenerates. Female orangutans have been shown to have a reproductive cycle of around seven years and are receptive for approximately six months before conception (Knott et al. 2009). In the model, females therefore have a cycle of seven years. They are randomly allocated a time within this cycle at the beginning of the simulation and when they reach the end of six and half years they become receptive for six months.

Each time step, individuals move according to rules specific to their age/sex class. Individuals move the length of one patch per time step, equivalent to 50 metres. It is assumed that all individuals know the location of flanged males from hearing long-calls, which can travel over large distances (Galdikas 1981, Galdikas 1983). Flanged males have a rank, and subordinate flanged males avoid dominant flanged males by retreating from them if they are within 100m, equal to the length of two patches (Figure 5.1). Otherwise, flanged males move toward the most productive food patch in their range (taking into account the distance to get there, see Appendix G for more details); orangutans have been shown to have spatial memory (Macdonald and Agnes 1999, Scheumann and Call 2006) and so are assumed to have a memory of their range and therefore know where the most productive trees are at any point in time within their range. Females have also been shown to avoid flanged males (Morrogh-Bernard 2009) and so this is also included in the model. If there are no flanged males nearby, females move to the most productive food patch (Figure 5.2), unless they are receptive in which case they seek out the highest ranking flanged male in their range and consort with him for five days - this is the mean length of consortships (Galdikas 1981) and oestrous (Nadler 1988). After this they remain apart for 23 days (simulating a 28 day cycle; Nadler 1988) and then seek a flanged male to consort with again.

Unflanged males avoid flanged males as their first priority (Figure 5.3). Unflanged males are assumed to be attracted to females. If they meet a receptive female (within 100m) they will remain with her for as long as possible (unless she is with a flanged male). Unflanged males are also attracted to non-receptive females. At Tanjung Puting, unflanged males were found to stay with adult females for around one day and adolescent females for around one week (Galdikas 1985a, Galdikas 1985b). The unflanged males in the model are programmed to behave in the same way towards non-receptive females. If the female leaves the territory of the male, or if a flanged male joins the group, the pair will split up, which means that the length of time these associations last varies considerably within the restrictions set. If unflanged males have no flanged males or females within a 100m radius, they will move to the most productive feeding patch.

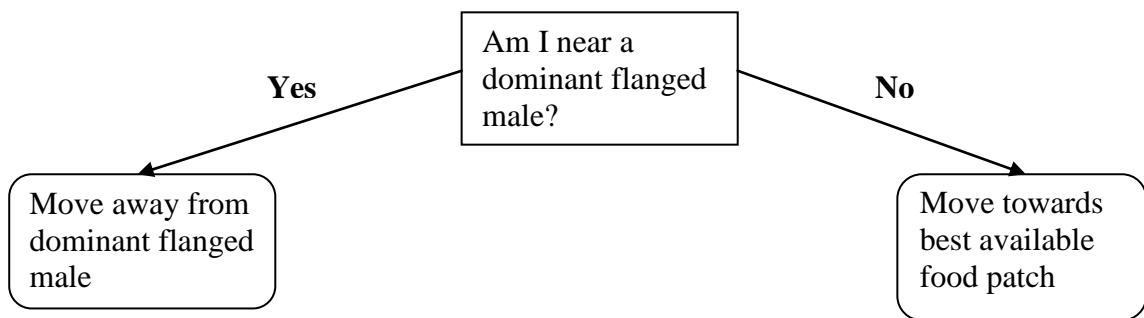


Figure 5.1: Flow chart of rules determining flanged male movement at each time step in the agent based model

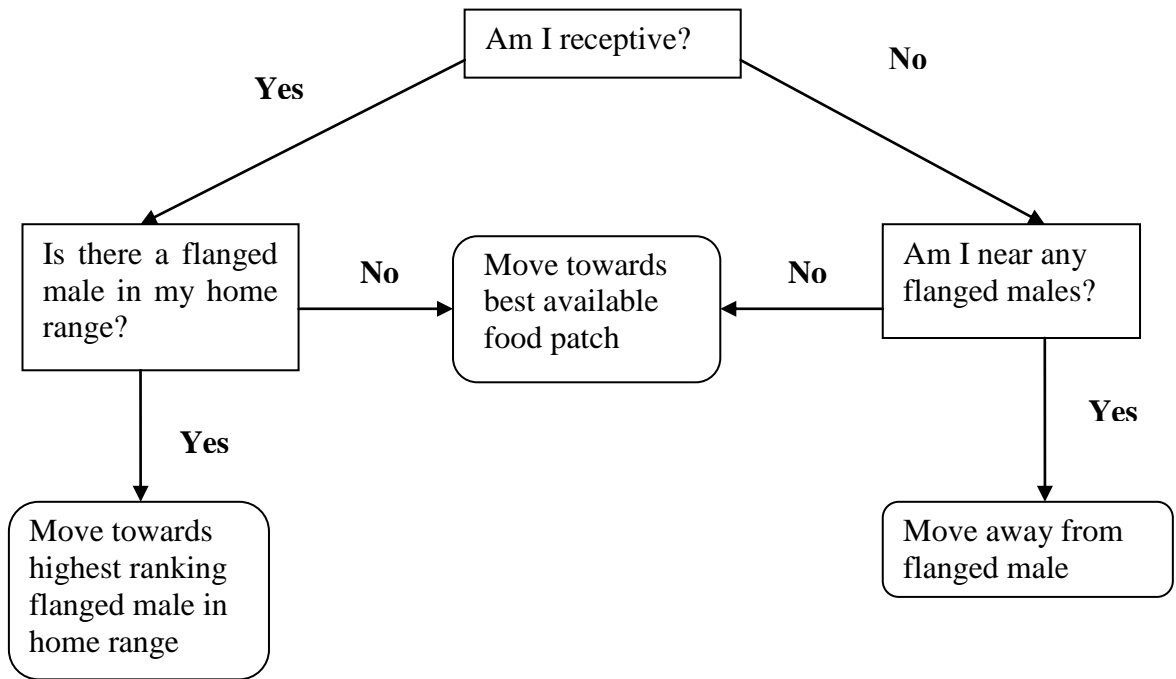


Figure 5.2: Flow chart of rules determining female movement at each time step in the agent based model

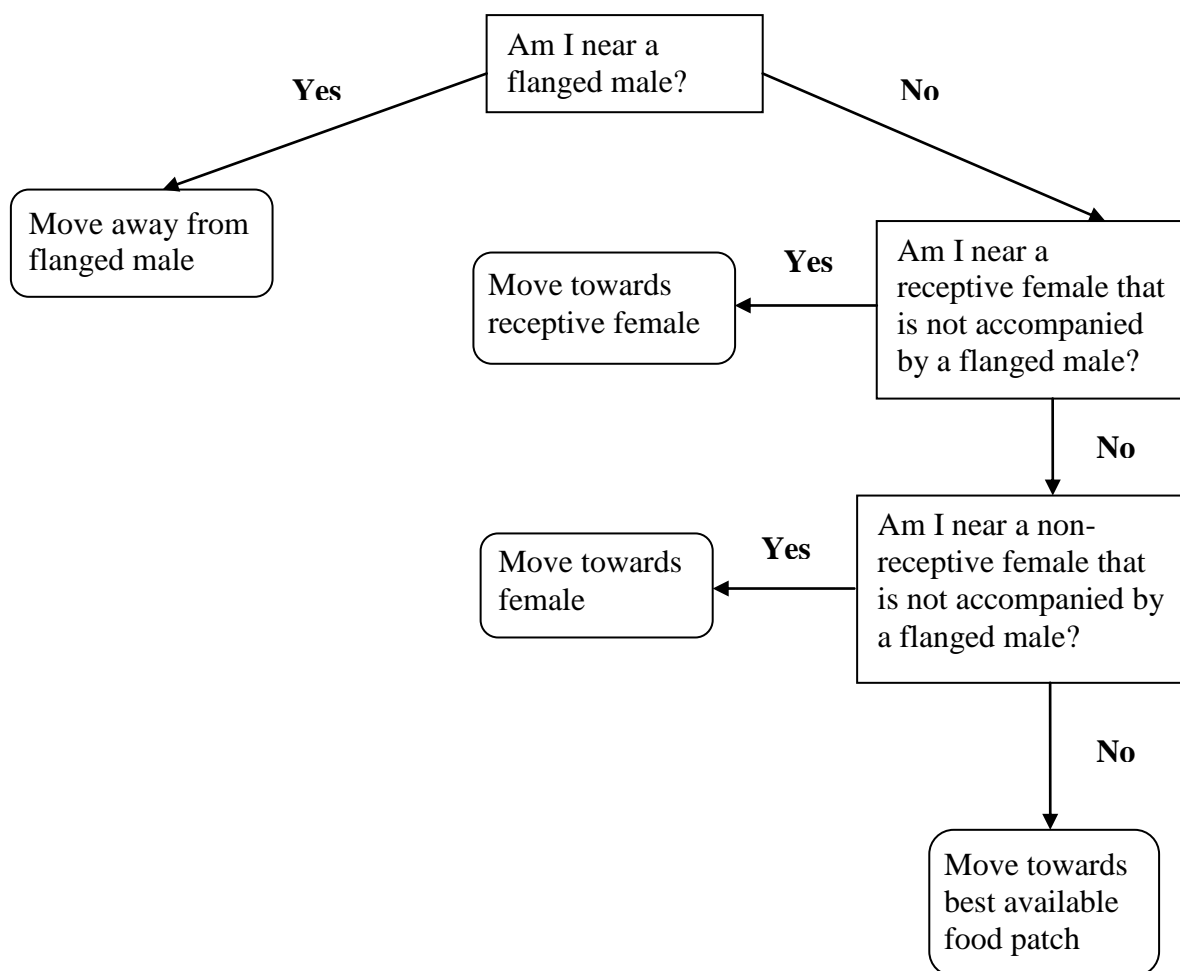


Figure 5.3: Flow chart of rules determining unflanged male movement at each time step in the agent based model

5.2.4.3 Disease transmission

At each time step disease also spreads from infected individuals to susceptible individuals that are within 50m of them, with a probability equal to the transmission coefficient of the disease modelled. Individuals recover with a probability equal to the recovery coefficient of the disease.

5.2.4.4 Initialisation

Each day is made up of 24 time steps, equal to a 12 hour day (sleeping is not considered in the model). The model was run for nine years (one month was set as 30 days for simplicity). At the beginning of the simulation, one individual is infected at random.

5.2.4.5 Model validation

The model was validated by extracting information about the time spent in parties, mean group size, mean daily distance travelled and percentage of time spent feeding on fruit, flowers and leaves from the agent based model and comparing these values with those found in reality at Sabangau. Focal observations were then simulated on the model, based on the actual number of focals performed on each individual over the nine year study period. An association network was extracted based on the data collected during these simulated focal observations, and compared with the actual association network from Sabangau (see Appendix G for full details).

5.2.4.6 Simulations of disease spread

Simulations were run for diseases with a range of realistic recovery times: one day, one week, two weeks, one month and six months. As very little is known about the value of transmission coefficients in reality, each of these diseases was run with varying transmission coefficients. The transmission coefficients were varied from one tenth of the recovery coefficient to ten times the recovery coefficient, as simulated on the static network. This therefore simulates a range of diseases where the probability of transmission per contact is lower than the probability of recovery per time step and

those in which the probability of transmission is higher than the probability of recovery.

Overall, these simulations should represent a wide range of potential diseases.

5.3 Results

The results for the orangutan static network are presented first, followed by the results for the chimpanzee static network and then the chimpanzee dynamic network. Lastly, the results for the orangutan agent based model are presented. Error bars are not shown in any of the figures as the standard errors of the 10,000 simulations used in all analyses are too small to be visible.

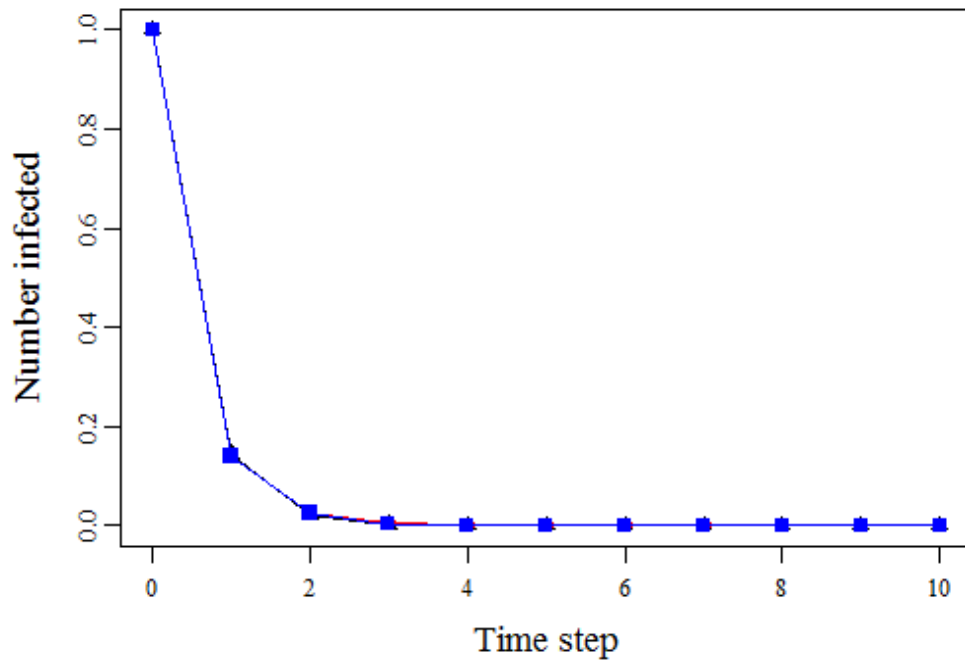
5.3.1 *The static orangutan SIR model*

5.3.1.1 *The effect of the topology of the network on predicted disease spread*

The number of individuals that were infected at each time step of the orangutan static model, the mean-field model and the random model is displayed in Figure 5.4a, and the number of recovered individuals at each time step is displayed in Figure 5.4b. In these models, transmission and recovery coefficients were 1.0. Disease was never found to survive for longer than four time steps within the static orangutan SIR model. Over 10,000 simulations, disease failed to spread beyond the initial infected individual in over 97% of runs. In fact, in only five of the 10,000 runs did disease reach the fourth time step. The average final size of the epidemic (i.e. the total number of individuals that contracted the disease) was 1.170. The most orangutans ever to become infected was seven and this occurred in only one simulation. Interestingly, the results from both the mean-field model and the random networks were very similar to each other and to the static model; disease also failed to spread and was extinct in all runs by the 5th time

step. The mean field model predicted the same final size of the epidemic of 1.170 while the random model predicted a marginally larger epidemic affecting an average of 1.173 orangutans. The overall conclusion of very little disease spread, however, remains the same under all models, suggesting that the inclusion of heterogeneity in contact patterns does not lead to different predictions. This indicates that a simple model based on homogenous mixing would be sufficient to predict disease dynamics in the orangutan population.

a)



b)

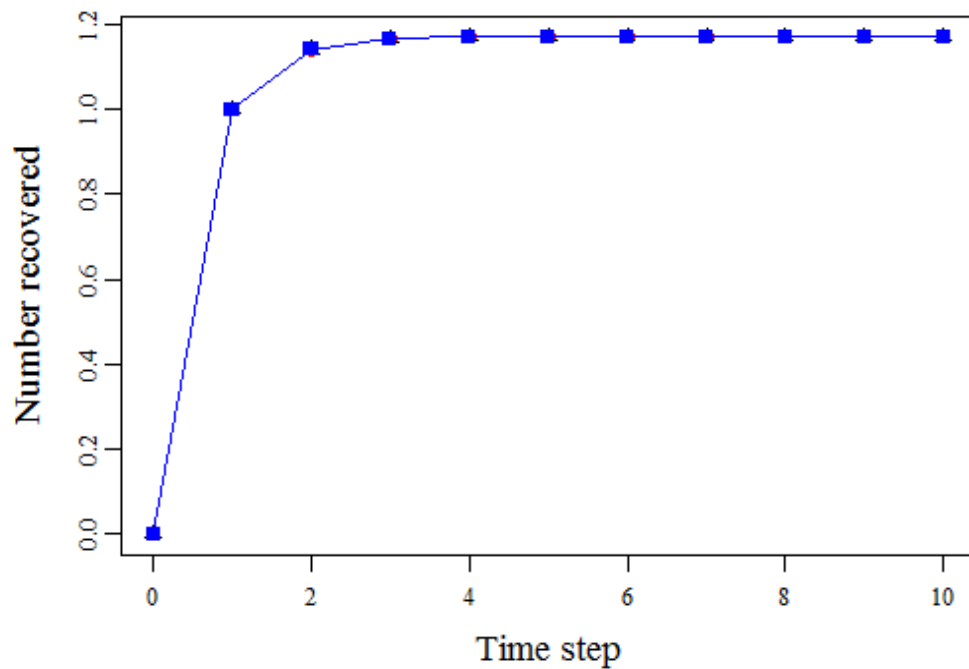


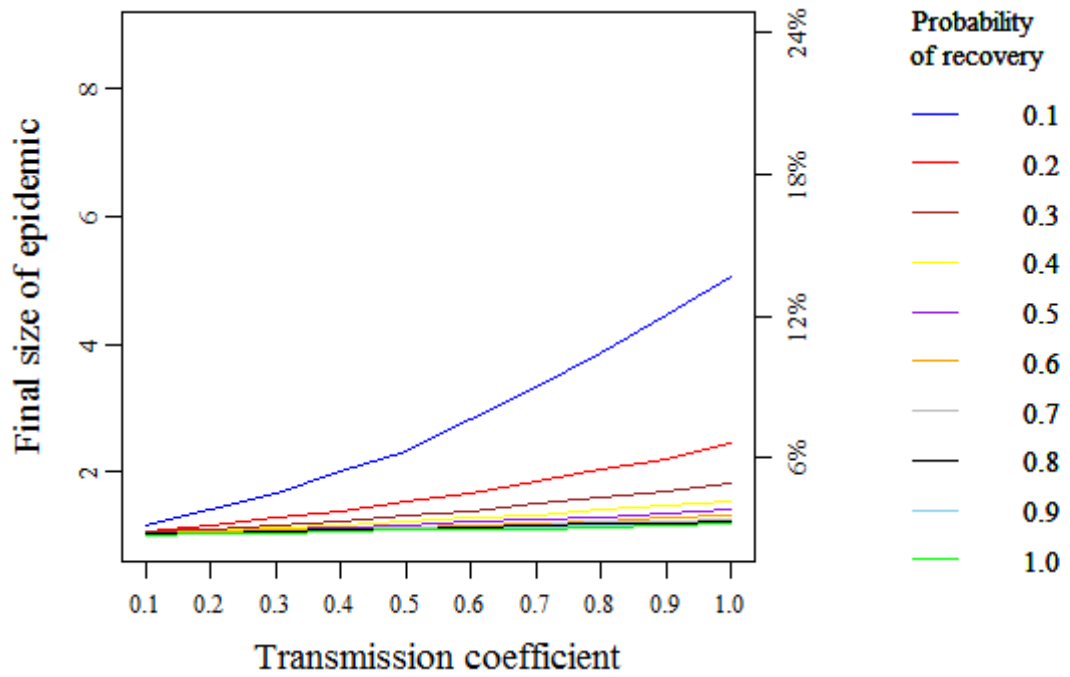
Figure 5.4: The average number of individuals that were a) infected and b) recovered at each time step in the SIR model using the orangutan data ($N=37$). Blue squares represent simulations on the actual orangutan network, black triangles the mean-field model and red circles the average from the random networks. Where only one colour is visible, networks produced the same, or extremely similar, results.

5.3.1.2 The spread of diseases with varying probabilities of transmission and recovery

The orangutan association network was found to be robust against the spread of diseases with a range of parameters; even with a very low probability of recovery of 0.1 per time step and a very high transmission coefficient of 1.0, on average only five of the orangutans become infected (Figure 5.5a). The network is particularly robust against diseases with high probabilities of recovery, as even with very high transmission coefficients, these diseases on average fail to spread to even one orangutan.

All combinations of the transmission coefficient and the probability of recovery produced almost identical results on the mean-field network as those on the association network (Figure 5.5b). The only exception was diseases with very low recovery ($\gamma=0.1$) and high infectiousness ($\beta>0.6$), but even here, the greatest difference found between the predictions was less than four individuals (c.10% of the population). For the majority of diseases, detailed association data do not therefore appear necessary to gain an impression of the number of orang-utan that are likely to be infected.

a)



b)

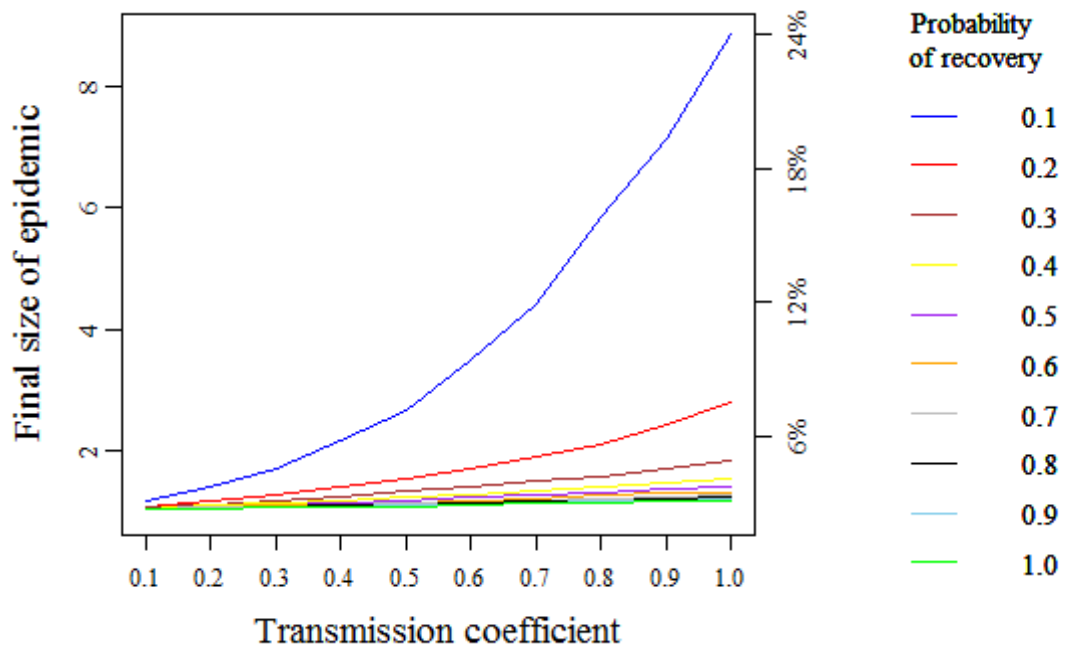


Figure 5.5: The final size of the epidemic in terms of absolute size and the percentage of the population, with different combinations of transmission and recovery probabilities in a) the orangutan static association network and b) the orangutan mean-field network.

5.3.1.3 The effect of individual network centrality on both the ability to transmit disease and individual infection risk

It is clear that for a disease with $\beta=1.0$ and $\gamma=1.0$ all four binary measures of centrality are strongly and significantly associated with the mean number of secondary infections, indicating that individuals with higher binary centrality have a greater probability of infecting others in the network (Figure 5.6). All four weighted measures of centrality are also strongly and significantly associated with the mean number of secondary infections (Figure 5.7). The proportion of variation explained was higher for the weighted measures than their binary counterparts. This suggests that weighted metrics may be more useful measures of a node's ability to infect others. The relationships between strength, weighted betweenness and weighted eigenvector centrality and the number of secondary infections were linear or quadratic while the relationship with weighted closeness centrality was exponential. Consequently, at high levels of weighted closeness centrality, small increases correlate with large increases in the mean number of secondary infections. All values were very low, however, and so absolute differences between individuals in both the ability to transmit disease and infection risk were minor. The results were very similar when the spread of a disease with a transmission coefficient of 1.0 and a recovery coefficient of 0.1 was simulated, i.e. disease parameters that led to maximum disease spread in this network (Appendix H). It is clear that varying the disease parameters has little effect on the results and that centrality in the orangutan network is associated with the ability to infect others under both types of disease. Although R^2 values and the shapes of the associations vary, overall the relationship between centrality and secondary infections is robust.

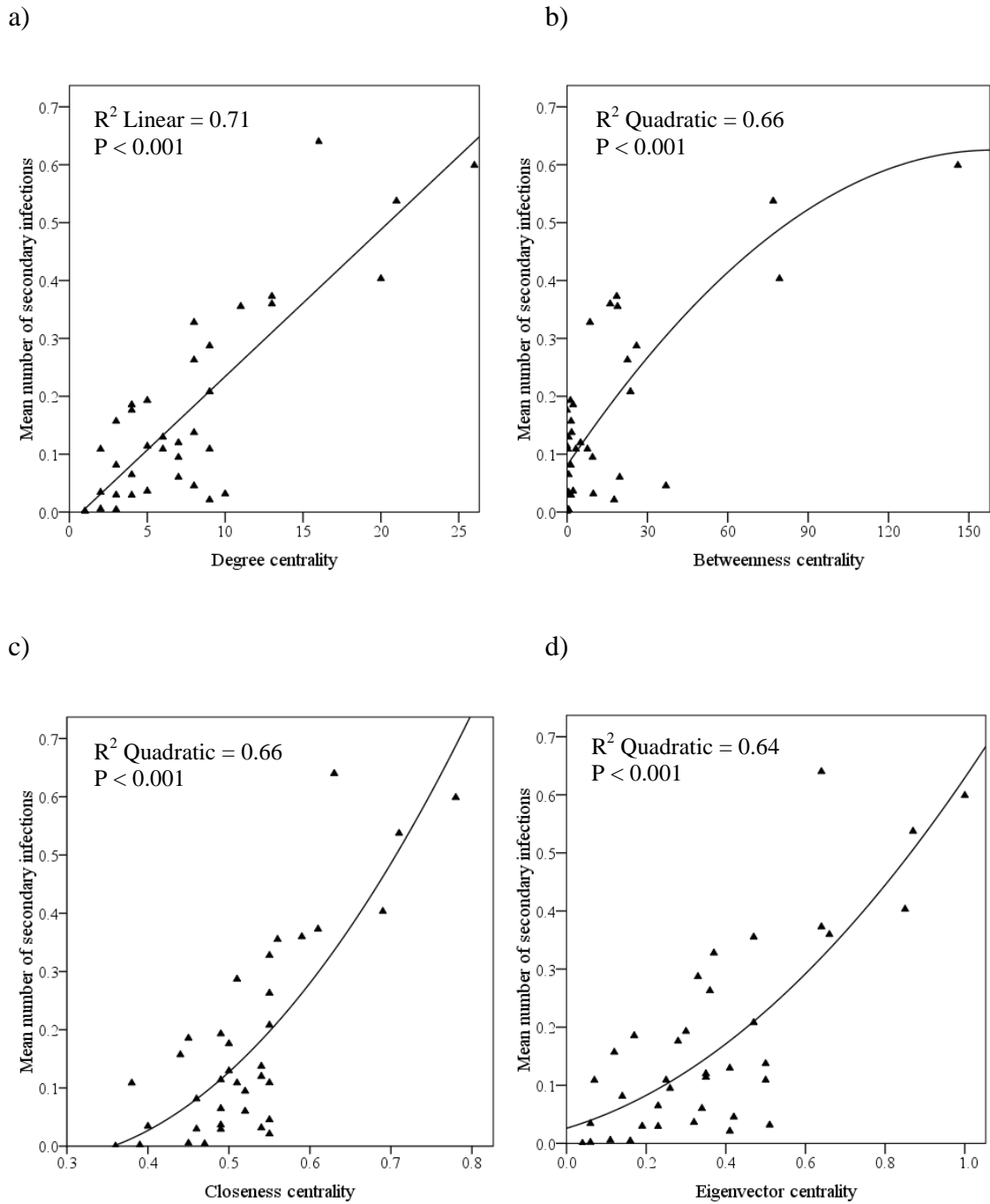


Figure 5.6: Mean number of secondary infections plotted against the a) degree, b) betweenness, c) closeness and d) eigenvector centrality of patient zero for the orangutan network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

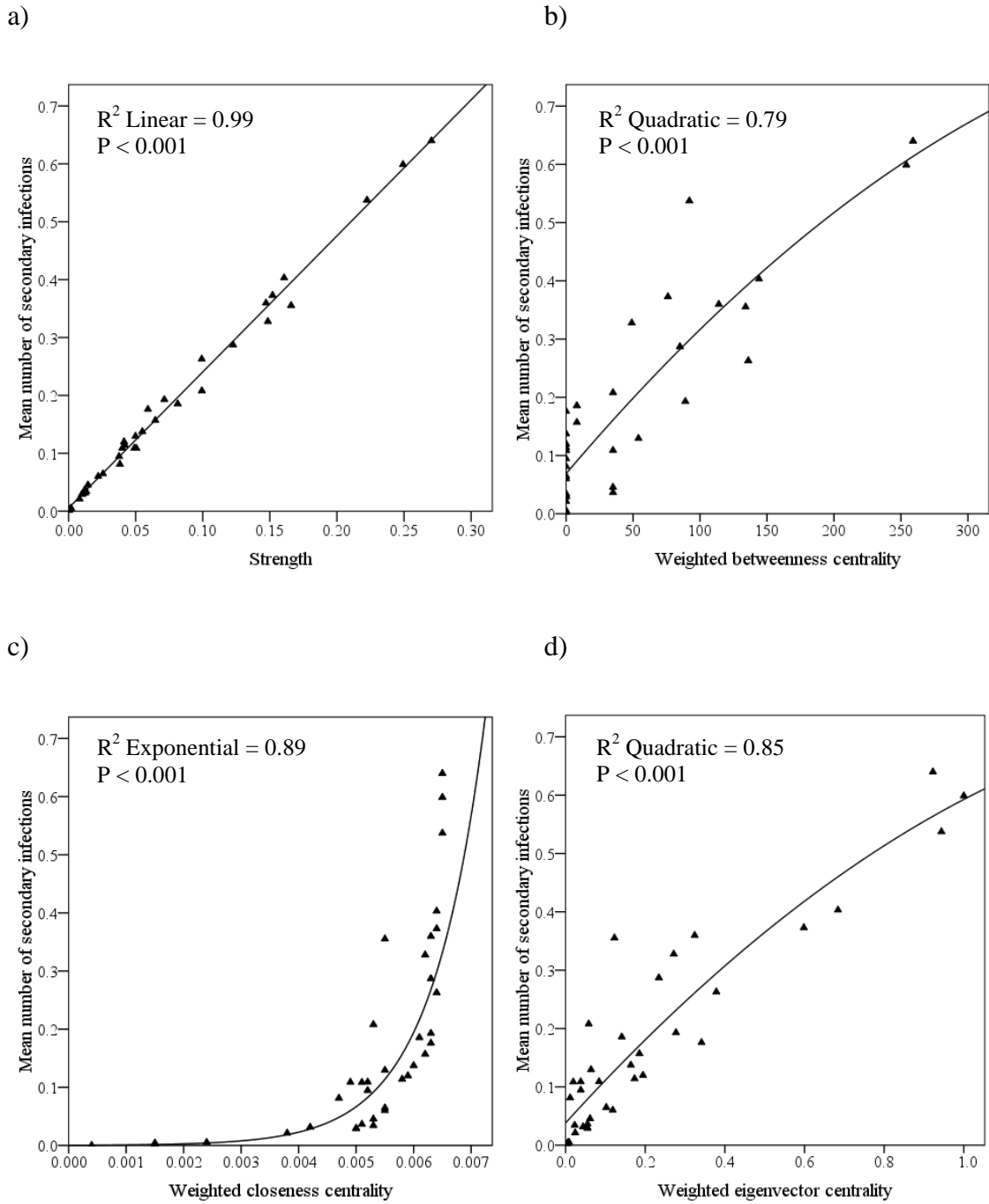


Figure 5.7: Mean number of secondary infections plotted against the a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality of patient zero for the orangutan network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

The effect of centrality on the probability of becoming infected was then explored. The risk of infection (i.e. the percentage of 10,000 simulations in which an individual became infected) plotted against the four binary centrality measures is displayed in Figure 5.8 and the four weighted measures in Figure 5.9 for a disease with β and γ of 1.0. The patterns are very similar to those between centrality and the number of secondary infections; all measures of centrality are significantly associated with infection risk. The relationship between weighted closeness centrality and infection risk is again exponential. These analyses were repeated simulating a disease with a transmission coefficient of 1.0 but a much slower recovery of only 0.1 and the results were similar (Appendix H). Overall, there is a clear association between both binary and weighted measures of centrality and infection risk, but again absolute values are extremely small for all individuals.

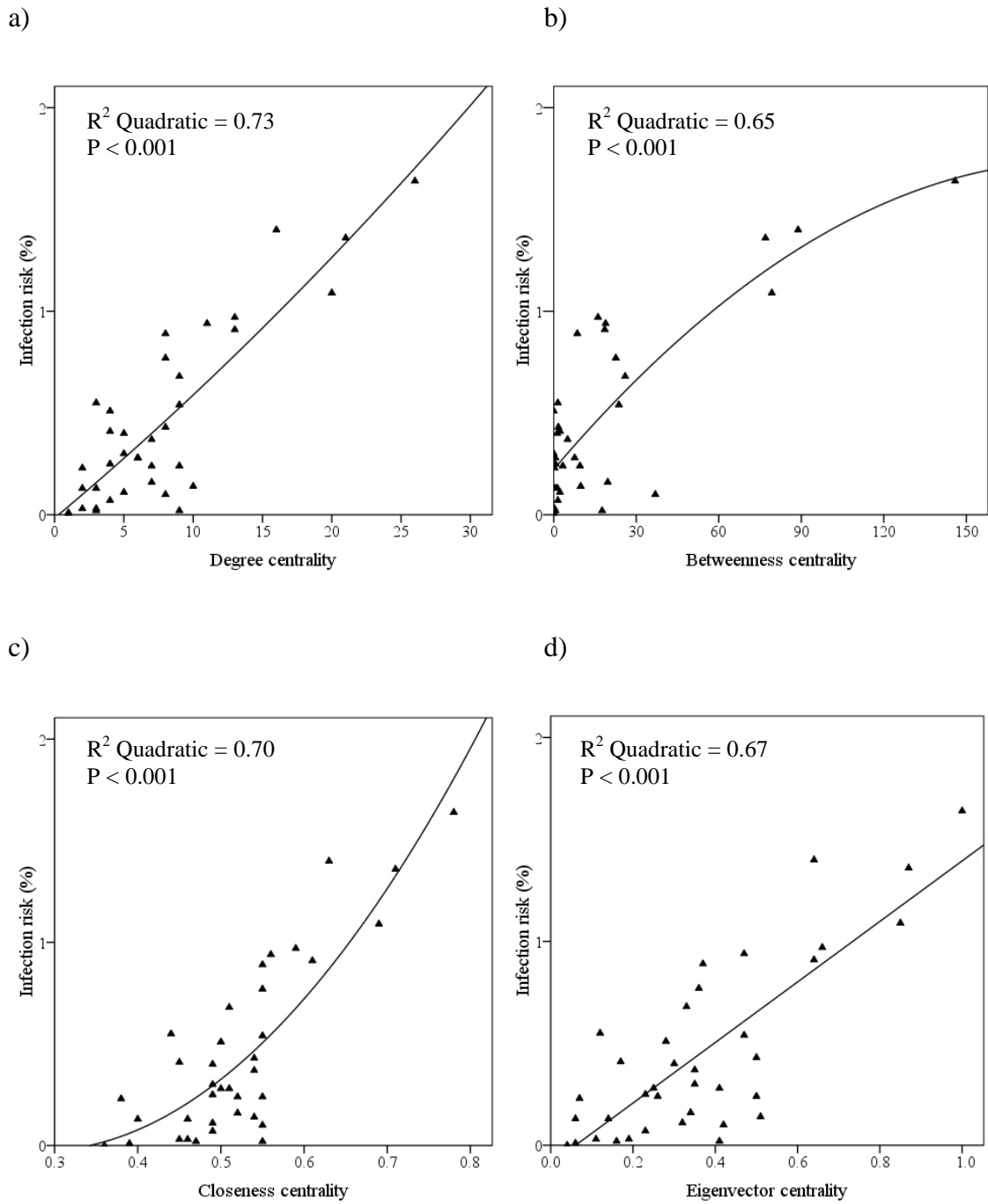


Figure 5.8: Infection risk (percentage of simulations in which an individual became infected) plotted against a) degree, b) betweenness, c) closeness and d) eigenvector centrality for the orangutan network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

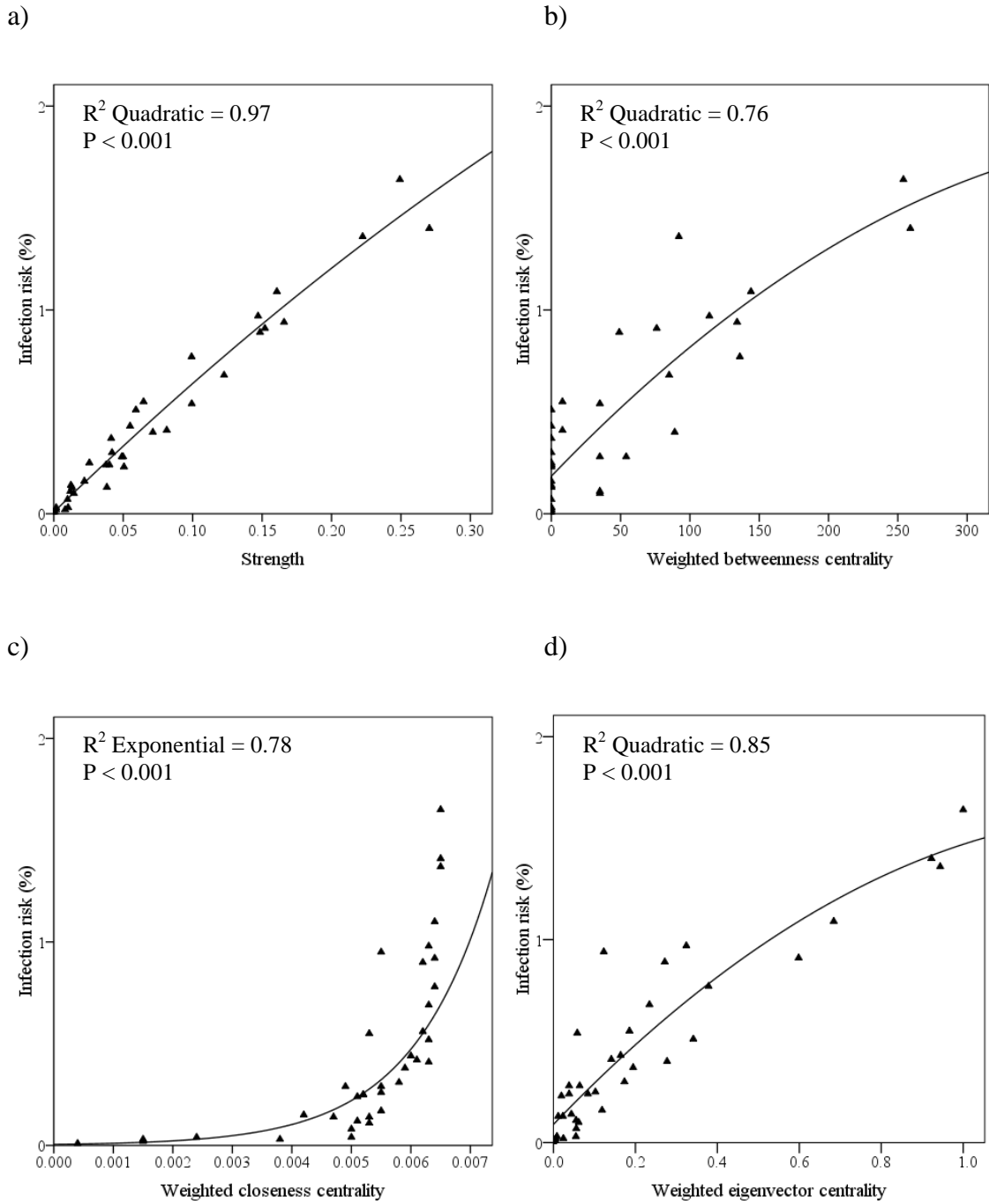
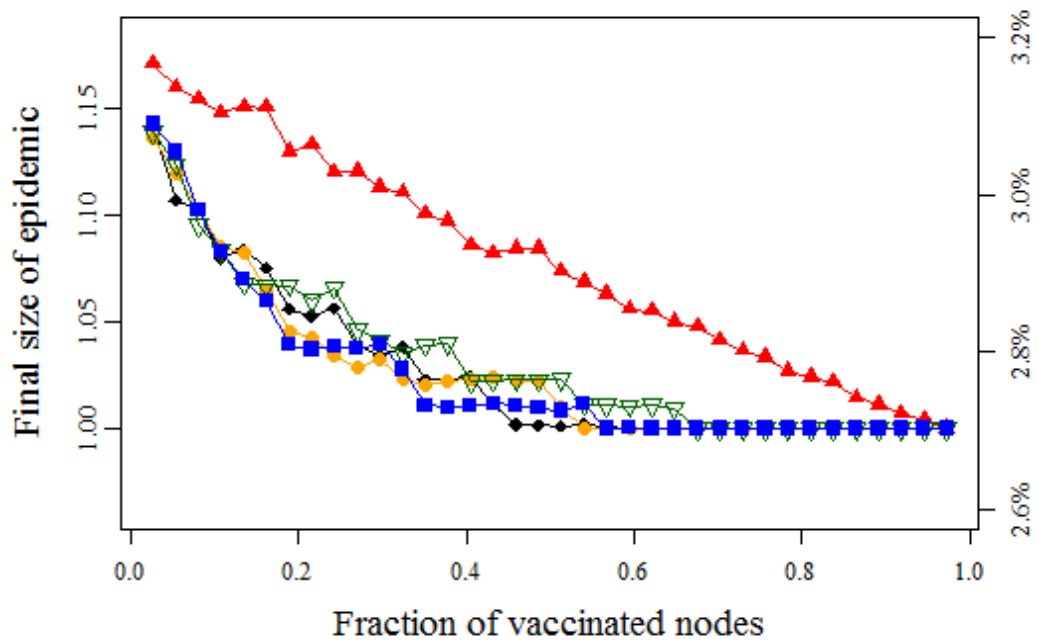


Figure 5.9: Infection risk (percentage of simulations in which an individual became infected) plotted against a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality for the orangutan network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

5.3.1.4 The value of random and targeted vaccination strategies on reducing disease spread

The final sizes of the epidemics following random vaccinations and following targeted vaccinations of individuals with high binary measures of centrality, are displayed in Figure 5.10a and the results of targeted vaccinations of those with high weighted centrality are shown in Figure 5.10b. The results are from the simulation of a disease with parameters $\beta=1.0$ and $\gamma=1.0$. The model was also run using a disease with parameters $\beta=1.0$ and $\gamma=0.1$ (i.e. the parameters that resulted in maximum disease spread) and the pattern was very similar (Appendix I). Targeting individuals with high centrality is clearly a more effective way of reducing the final size of the epidemic than targeting individuals at random, although the absolute difference is minimal. All four methods of targeted vaccination produce fairly similar results. Of the weighted measures, strength and weighted betweenness centrality appeared to have the strongest effect on the final size of the epidemic. In both simulations, targeting between 50-60% of individuals with high degree/strength or betweenness/weighted betweenness completely prevents disease from spreading beyond patient zero.

a)



b)

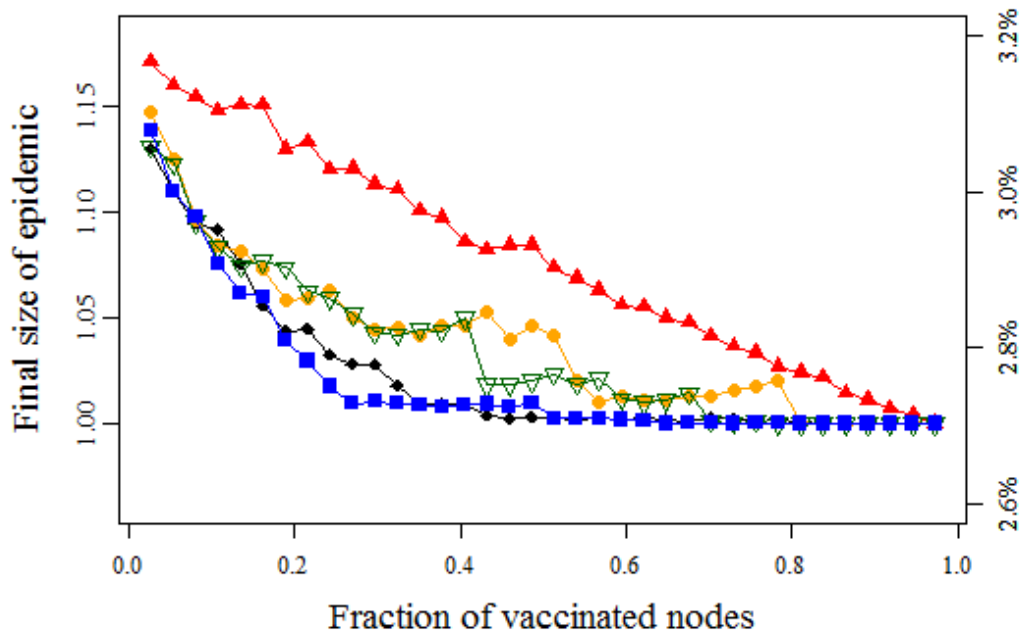


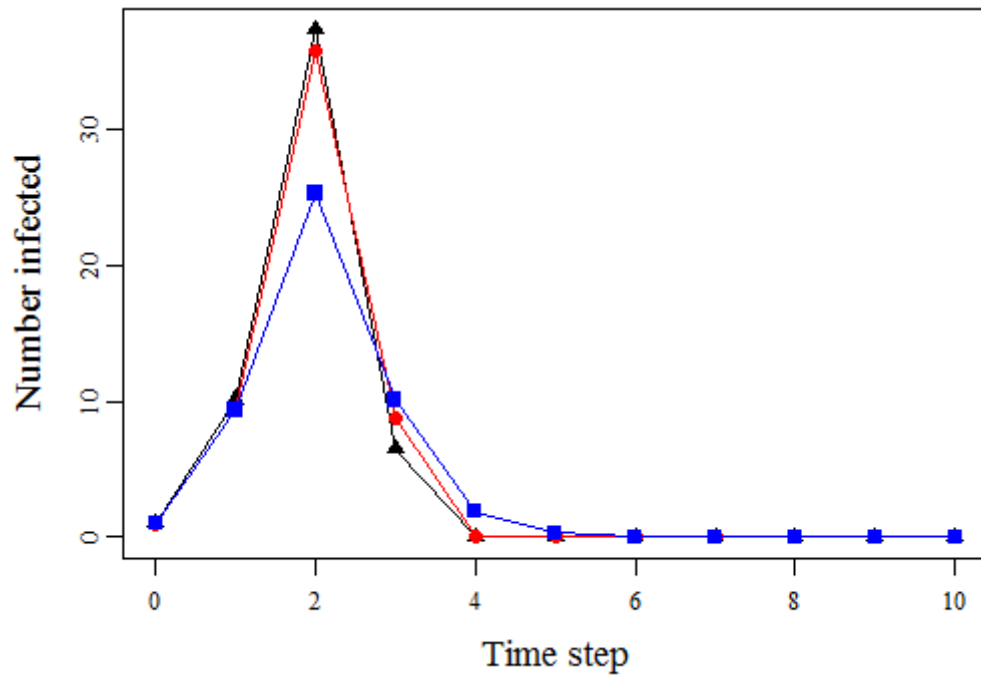
Figure 5.10: The final size of the epidemic following the vaccination of different proportions of the population in the orangutan network. In a) targeted vaccinations are based on binary measures of centrality, in b) weighted measures. Red triangles indicate random vaccinations, blue squares indicate targeted vaccinations of individuals with high degree/strength, black diamonds individuals with high betweenness/weighted betweenness, yellow circles individuals with high closeness/weighted closeness and green inverted triangles individuals with high eigenvector/weighted eigenvector centrality.

5.3.2 The static chimpanzee SIR model

5.3.2.1 The effect of the topology of the network on predicted disease spread

The results for the chimpanzee network were in stark contrast to those for the orangutan network. The number of individuals infected at each time step is displayed in Figure 5.11a and the number recovered in Figure 5.11b. In a very short number of time steps, disease spread to a high proportion of network members. In fact, by only the second time step in the association network, 25.3 chimpanzees were infected on average (46% of the population). The disease then rapidly dies out; probably due to the high recovery rate (infected individuals always recover each time step). Overall, 48.1 individuals on average were infected (88% of the community). The pattern of disease spread was similar for the mean-field model, but the epidemic peaked at an average of 37.4 infected individuals, 68% of the population. The final size of the epidemic was 54.9, which means that in almost all simulations 100% of the community became infected. The average result from the 1000 random networks was very similar to the results from the mean-field model; the epidemic peaked at an average of 35.8 individuals (65% of the population) and the mean final size of the epidemic was 54.9. Incorporating heterogeneity in contact patterns therefore has an important effect on the results.

a)



b)

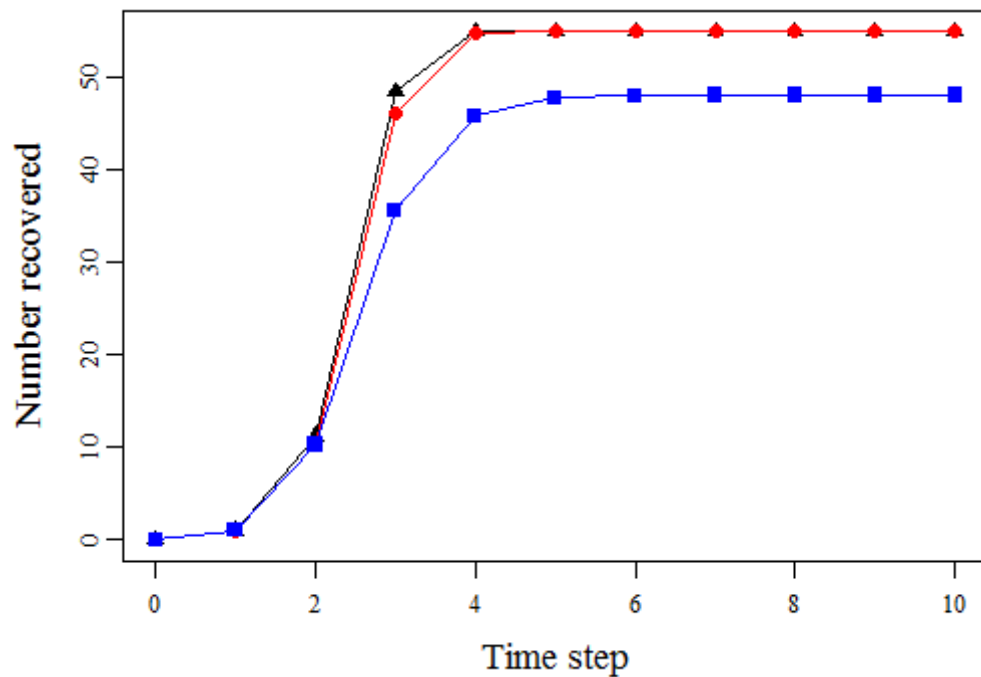


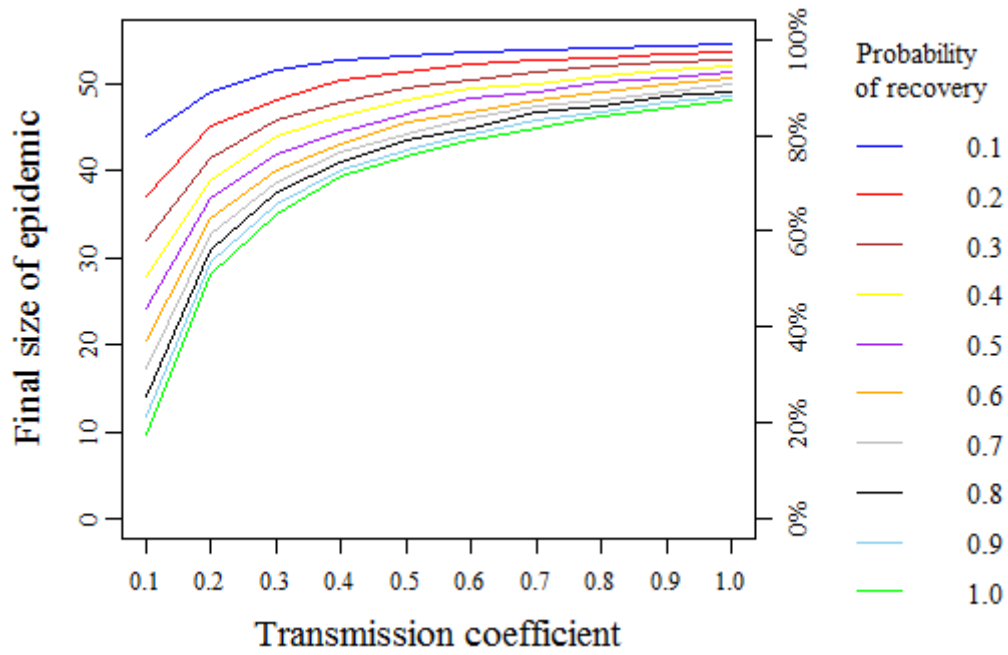
Figure 5.11: The average number of individuals that were a) infected and b) recovered at each time step in the SIR model using the chimpanzee data ($N=55$). Blue squares represent simulations on the actual chimpanzee network, black triangles the mean-field network and red circles the average from the random networks. Where only one colour is visible, networks produce the same, or extremely similar, results.

5.3.2.2 The spread of diseases with varying probabilities of transmission and recovery

Varying the transmission and recovery probabilities had marked effects on the final size of the epidemic in the chimpanzee network (Figure 5.12a). Diseases with a high probability of transmission, i.e. highly infectious diseases, spread to almost all of the chimpanzees in the network even when combined with a very high recovery probability. Indeed, even with certain recovery at each time step ($\gamma=1.0$), a disease only needs a transmission probability of 0.5 in order to reach over 40 members (73%) of the chimpanzee community on average. Diseases with a low probability of transmission combined with a high probability of recovery did not spread as much in the network; with the lowest tested value of 0.1 for transmission probability and the highest of 1.0 for recovery, the final size of the epidemic was 9.76 (17.7% of the population). Increasing the transmission coefficient led to large relative increases in the final size of the epidemic. Increasing the probability of recovery did not lead to such large increases in the total number infected by the epidemic. The chimpanzee network therefore appears to be susceptible to diseases with a range of parameters, but particularly to those with intermediate to high transmission coefficients.

Under almost all combinations of parameters, the final size of the epidemic on the mean-field network was higher than that on the association network (Figure 5.12b). Only diseases with very high recovery rates ($\gamma>0.7$) and low transmission coefficients ($\beta=0.1$) spread more on the association network than on the mean-field network. Excluding these combinations, on average an additional 7.53 chimpanzees, or 14% of the community (range 1-22%), were predicted to become infected on the mean-field network compared to the association network. Thus, incorporating heterogeneity in contact patterns has an important effect on predicted disease spread for the chimpanzee.

a)



b)

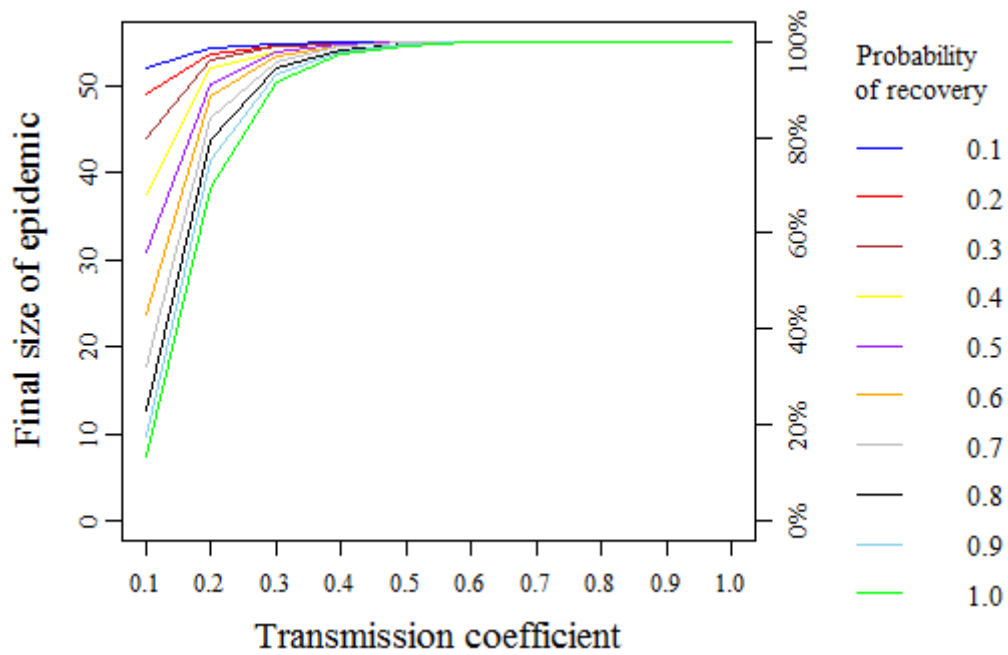


Figure 5.12: The final size of the epidemic in terms of absolute size and the percentage of the community, with different combinations of transmission and recovery probabilities, in a) the chimpanzee static association network and b) the chimpanzee mean-field network.

5.3.2.3 The effect of individual network centrality on both the ability to transmit disease and individual infection risk

The mean numbers of secondary infections when each chimpanzee was selected as patient zero were also calculated and plotted against the four binary and the four weighted centrality measures (Figures 5.13 and 5.14). The graphs clearly show that similar to the orangutan network, within the chimpanzee network there was a strong relationship between centrality and the ability to infect others and these associations were stronger using the weighted than the binary centrality measures (with the exception of weighted betweenness centrality). The correlations between betweenness/weighted betweenness centrality and the number of secondary infections were much weaker than for the other measures of centrality; indeed the relationship with weighted betweenness centrality was very weak and was not significant. Interestingly, the significant relationships between strength and number of secondary infections and weighted eigenvector centrality and number of secondary infections were both logarithmic. This suggests that increases in centrality had a greater impact on the number of secondary infections for less central individuals, whereas individuals with medium and high centrality shared a very similar ability to spread disease. The analyses were repeated using diseases with parameter $\beta=0.1$ and $\gamma=0.9$ and $\beta=0.1$ and $\gamma=0.4$, both of which produced similar, though stronger, correlations (Appendix J).

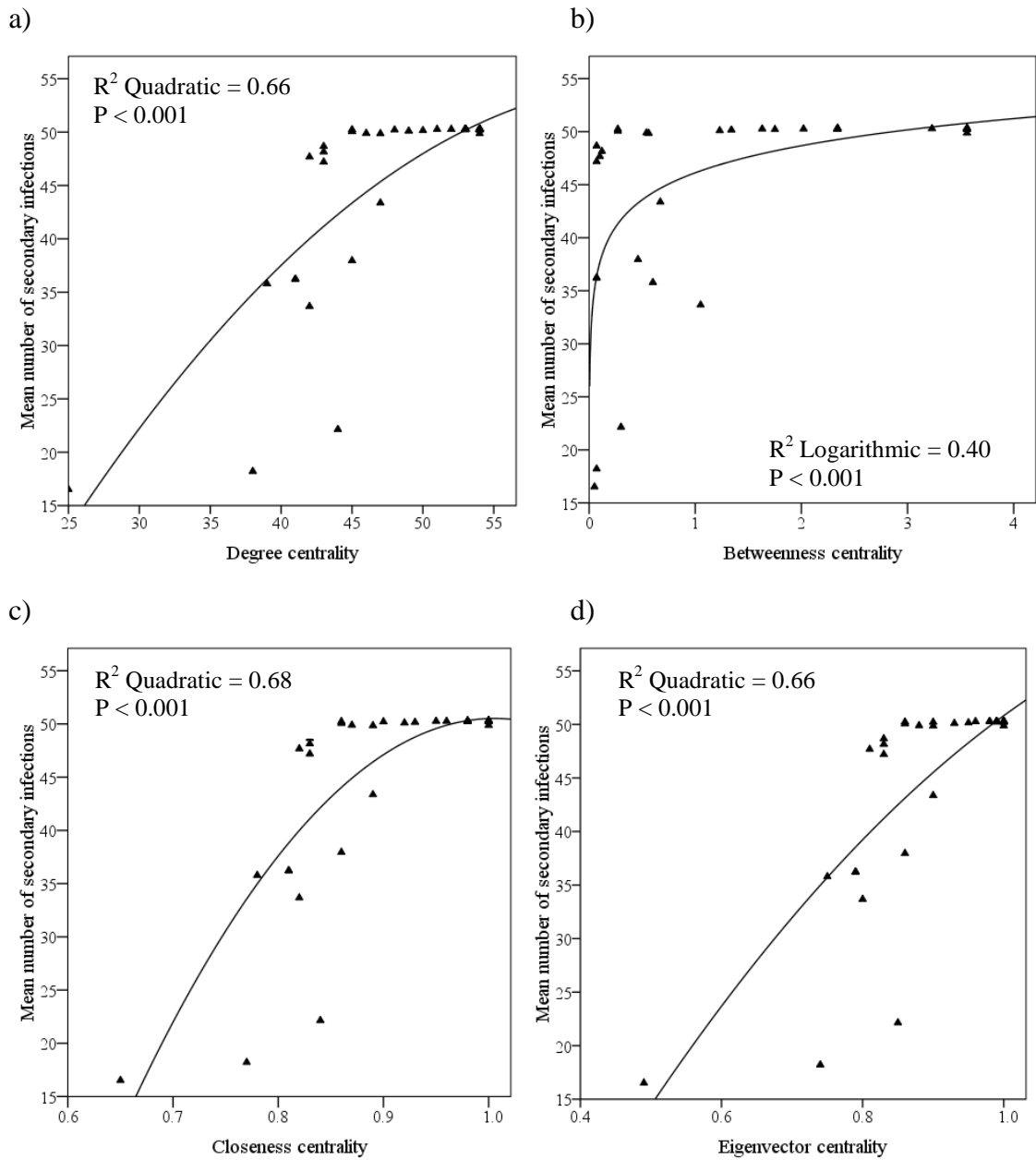


Figure 5.13: Mean number of secondary infections plotted against the a) degree, b) betweenness, c) closeness and d) eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

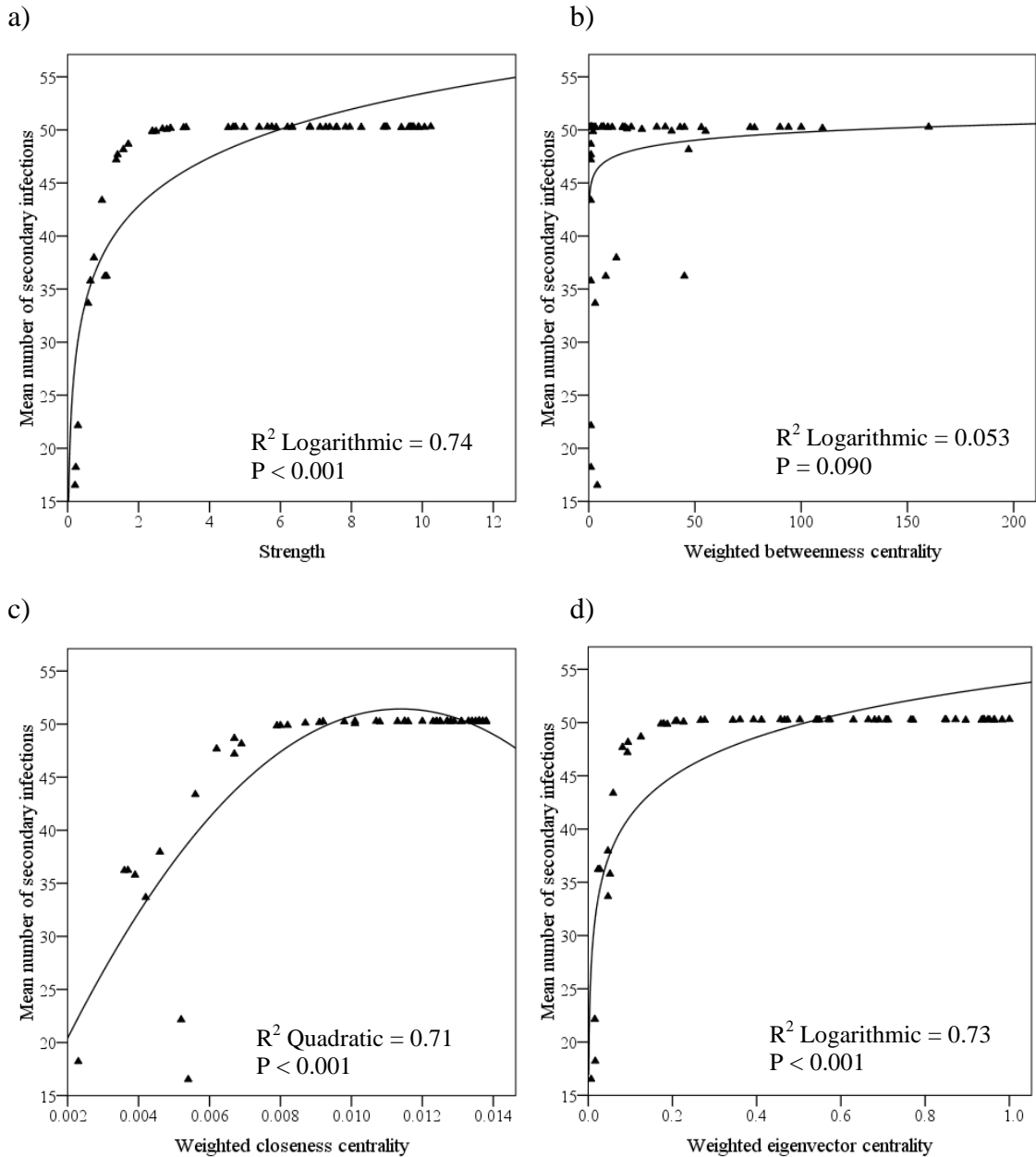


Figure 5.14: Mean number of secondary infections plotted against the a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

The relationship between infection risk and centrality was also explored. Figure 5.15 shows the associations between infection risk and degree, betweenness, closeness and eigenvector centrality, while Figure 5.16 shows the associations between infection risk and strength, weighted betweenness, weighted closeness and weighted eigenvector

centrality. The relationships were almost identical to those between the mean number of secondary infections and centrality, indicating that centrality affects both the ability to infect others and individual infection risk in the same way. Betweenness centrality and weighted betweenness centrality had weak relationships with infection risk and the latter relationship was not significant, but all other measures of centrality were positively and significantly related to infection risk. Again, the significant relationships between infection risk and strength, betweenness and weighted eigenvector centrality were logarithmic. The associations between infection risk and centrality remained when the disease parameters were varied (Appendix J).

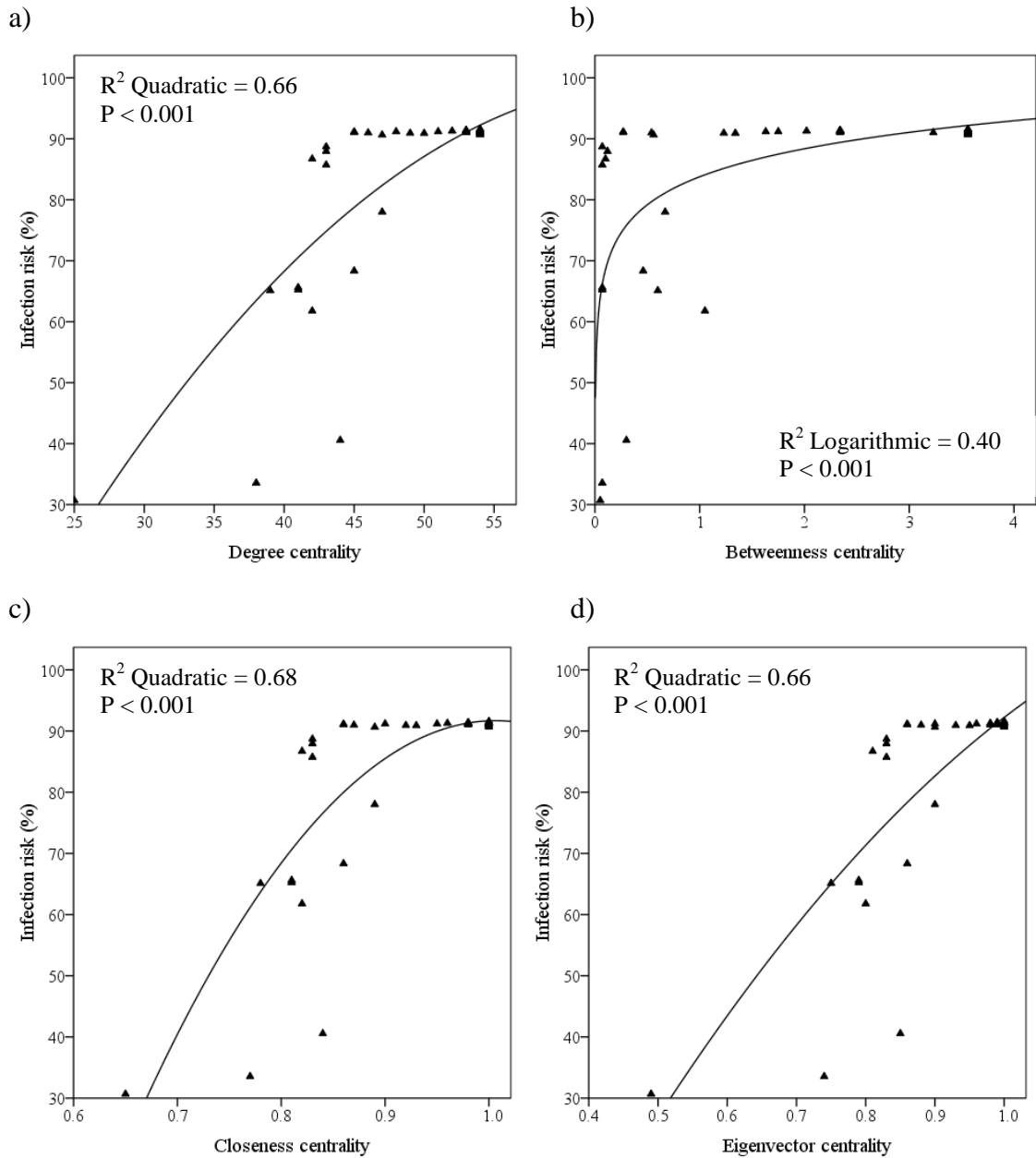


Figure 5.15: Infection risk (percentage of simulations in which an individual became infected) plotted against a) degree, b) betweenness, c) closeness and d) eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

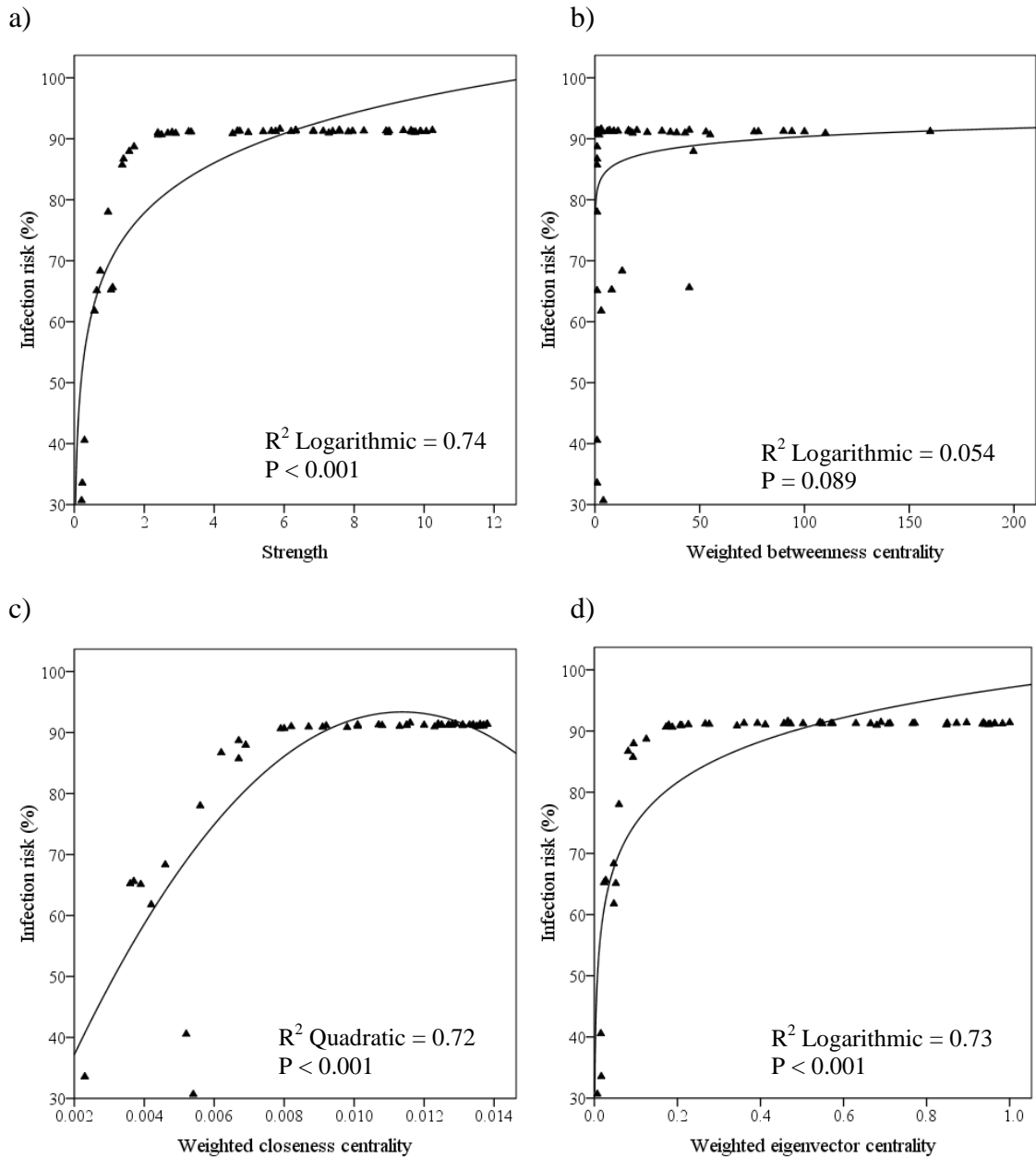
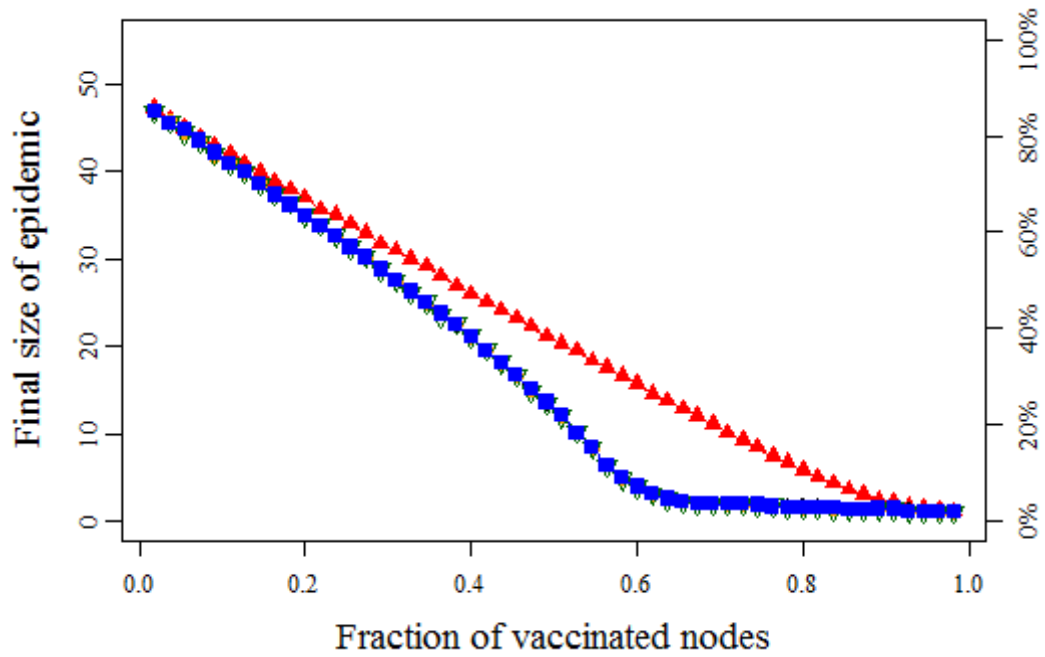


Figure 5.16: Infection risk (percentage of simulations in which an individual became infected) plotted against a) strength, b) weighted betweenness, c) weighted closeness and d) weighted eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=1.0$ and $\gamma=1.0$.

5.3.2.4 *The value of different vaccination strategies in reducing disease spread*

Vaccination had a clear effect on the final size of the epidemic (Figure 5.17). The figures show the simulation of a disease with parameters $\beta=1.0$ and $\gamma=1.0$. Under both random and targeted vaccinations (both of individuals with high binary and weighted centrality) the final size of the epidemic decreased as the fraction of vaccinated nodes increased, and this effect was stronger for targeted than random vaccinations. For the weighted measures, weighted betweenness centrality had a much smaller effect than the other three measures. The model was also run using parameters $\beta=0.1$ and $\gamma=0.9$ (i.e. the parameters that resulted in approximately 20% of individuals becoming infected) and parameters $\beta=0.1$ and $\gamma=0.4$ (i.e. the parameters that resulted in around 50% of individuals becoming infected). The pattern was very similar for all three simulated diseases (Appendix K). These results suggest that targeted vaccinations of around 60% of the chimpanzee community would prevent disease from spreading.

a)



b)

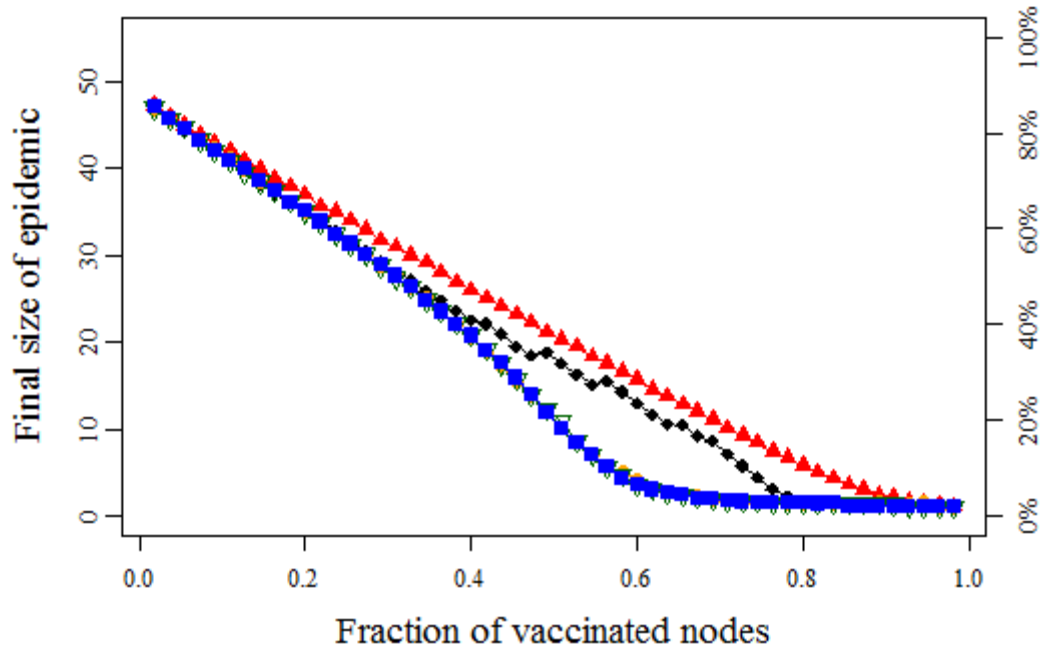
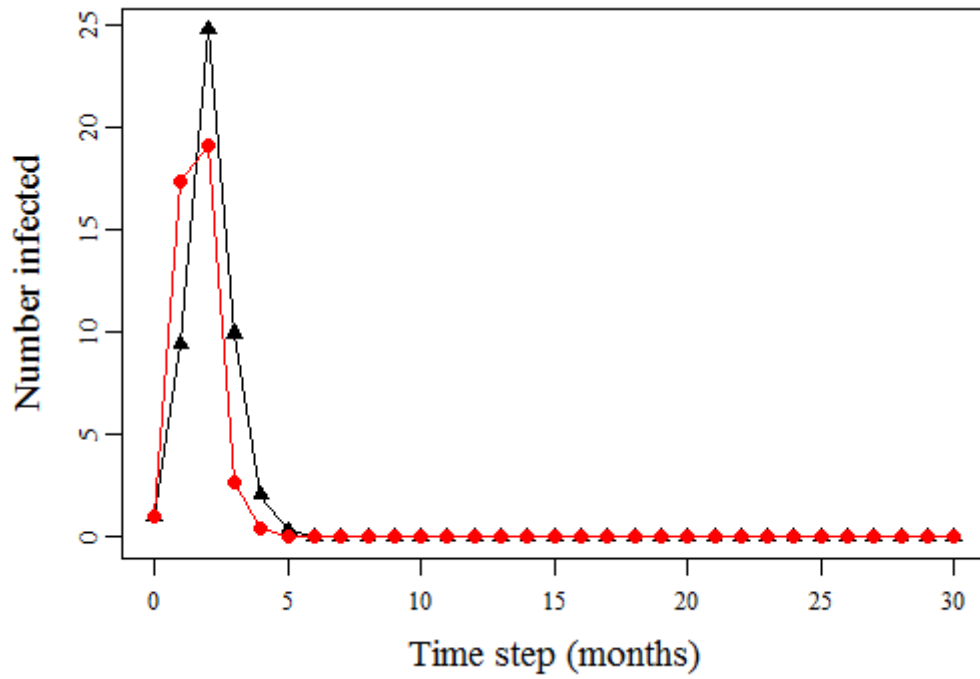


Figure 5.17: The final size of the epidemic following the vaccination of different proportions of the population in the chimpanzee network. In a) targeted vaccinations are based on binary measures of centrality, in b) weighted measures. Red triangles indicate random vaccinations, blue squares indicate targeted vaccinations of individuals with high degree/strength, black diamonds individuals with high betweenness/weighted betweenness, yellow circles individuals with high closeness/weighted closeness and green inverted triangles individuals with high eigenvector/weighted eigenvector centrality.

5.3.3 The importance of short-term relationships: the dynamic chimpanzee SIR model

The number of individuals that were infected at each time step under the dynamic model is displayed in Figure 5.18a. The number infected at each time step using a static model based on the 30 months of data is also displayed in Figure 5.18a for comparison. This is similar to the static model presented previously, but excludes data from the first six months so that it can be compared with the dynamic model. The number of individuals recovered at each time step under both dynamic and static models is displayed in Figure 5.18b. The static model predicted a larger epidemic, reaching a final size of 47.33 compared to 40.47 under the dynamic model.

a)



b)

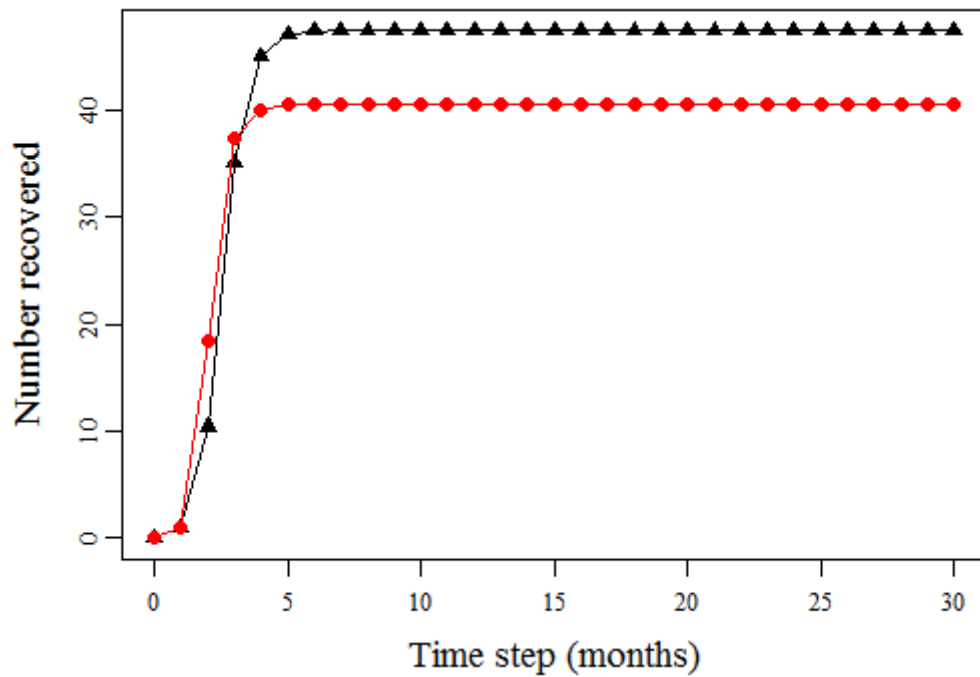


Figure 5.18: The number of a) infected individuals and b) recovered individuals at each time step using both the dynamic and the static models ($\beta=1.0$, $\gamma=1.0$, $N=55$). Black triangles represent the static model and red circles represent the dynamic model.

The probabilities of transmission and of recovery were then varied in both the dynamic model and the static model based on 30 months of data. The results from the dynamic model are displayed in Figure 5.19a and the results from the static network based on the same 30 months of data in Figure 5.19b. It is clear that in both models all diseases spread to a large proportion of group members, particularly those diseases with intermediate to high transmission coefficients. This confirms the susceptibility of the chimpanzee network to a range of diseases but particularly to those with a high probability of transmission. Comparing the results from the two models produced interesting results; at low transmission coefficients the dynamic model predicted slightly greater disease spread for all recovery values, while at high transmission coefficients the static model predicted considerably greater disease spread for all recovery values. Overall, the results were fairly similar between the two models. It is important to highlight that in both models the lines representing diseases with a probability of recovery of 0.1 predicted less disease spread at medium to high transmission coefficients than diseases with higher recovery. This was a result of the low number of time steps meaning that the final size of the epidemic could not be measured; this has a greater impact on diseases that spread slowly. If the number of time steps were extended, it is probable that the final size of the epidemic for diseases with a recovery of 0.1 would exceed that for diseases with faster recovery.

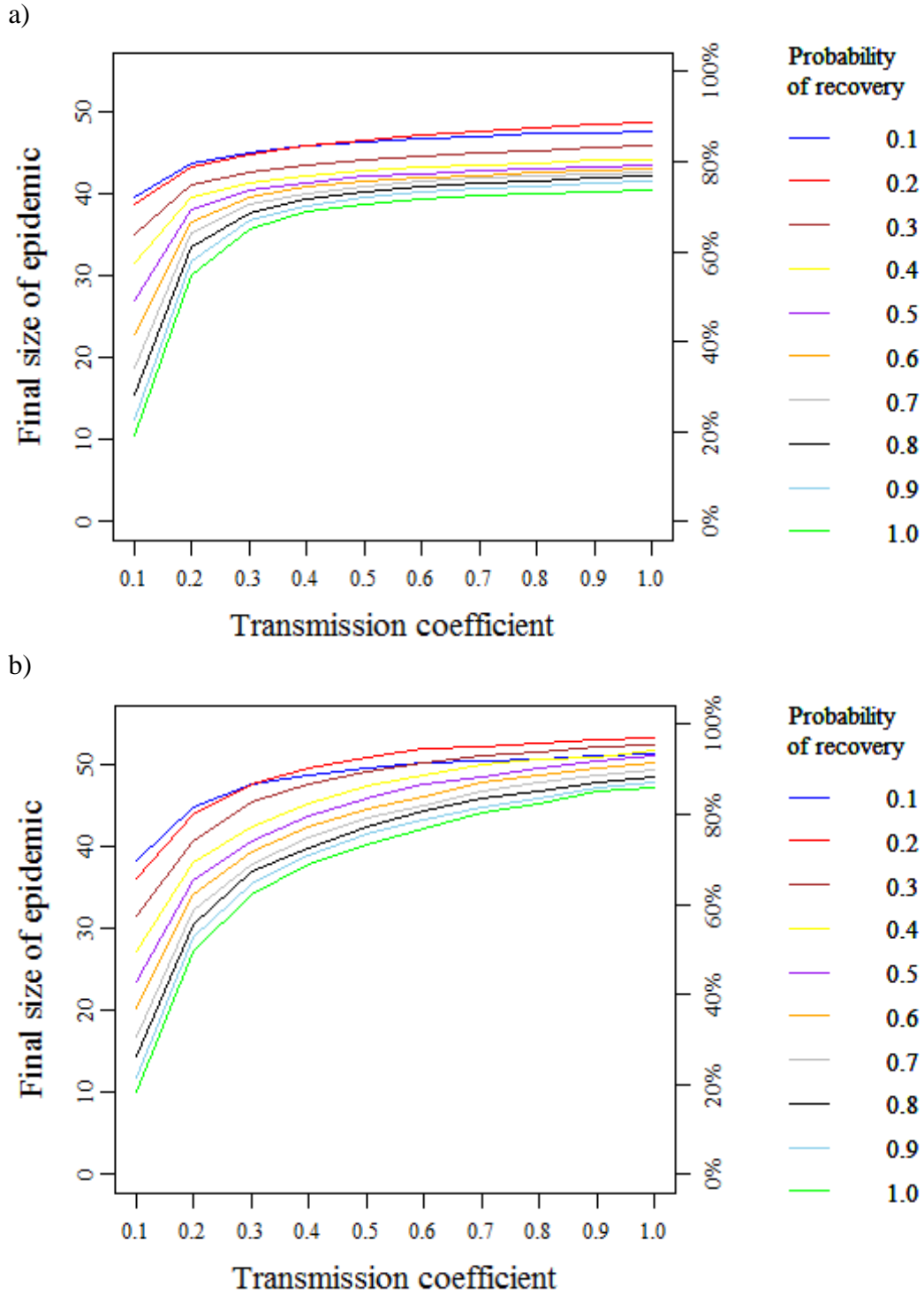


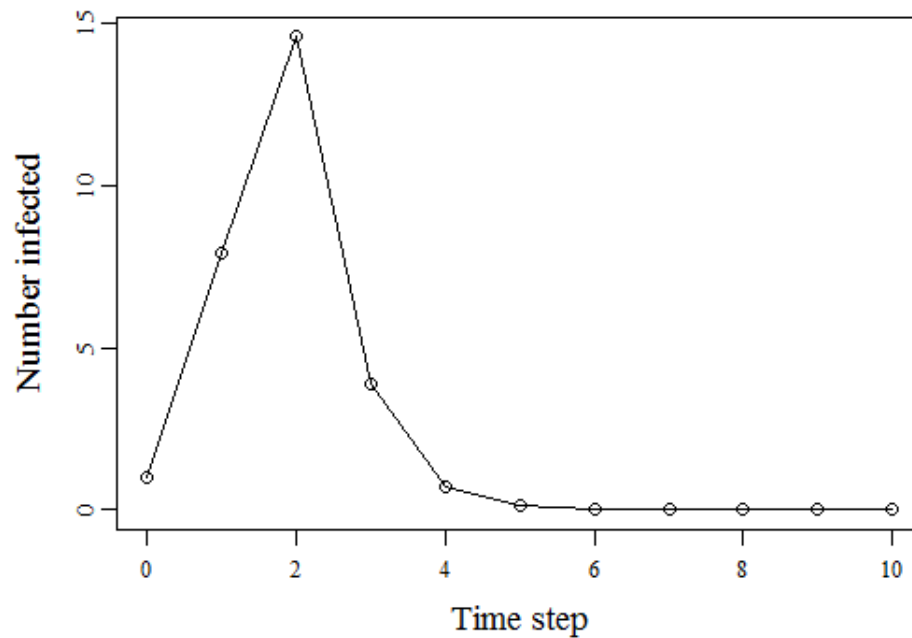
Figure 5.19: The size of the epidemic in terms of both absolute size and the percentage of the community after 30 time steps with different combinations of transmission and recovery probabilities in a) the chimpanzee dynamic network and b) the static network based on 30 months of data.

5.3.4 Diseases that spread over shorter time frames: the chimpanzee monthly networks

To investigate the way in which diseases with infectious periods shorter than one month would spread, whilst including the temporal variation in relationships between months, the spread of disease ($\beta=1.0$, $\gamma=1.0$) was simulated on each of the 30 networks individually. The average number of individuals that were infected at each notional time step over these 30 networks is displayed in Figure 5.20a and the average number that recovered at each time step in Figure 5.20b. Disease rapidly spread to a large proportion of the community when simulated over one month. Compared to the static model based on all 30 months of data (Figure 5.18), however, the final size of the epidemic was much less (28.30 ± 2.34 vs 47.33). As the number of individuals in each of the monthly networks was also less than that in the overall static network, on average this was 69% of individuals compared to 86% in the model based on all 30 months. This smaller predicted epidemic may indicate that diseases with recovery times shorter than one month may spread less than diseases that persist for longer or alternatively that the observation effort during one month in this dataset was not enough to collect sufficient data on chimpanzee relationships. Interestingly, however, there was no significant relationship between the number of focal scans performed per month and the predicted size of the epidemic ($r = -0.183$, $N = 30$, $P = 0.332$). There was also no significant relationship between the number of focal scans and either the number of edges in the network ($r = -0.257$, $N = 30$, $P = 0.171$) or the number of individuals in the network ($r = -0.109$, $N = 30$, $P = 0.566$). In addition, each of the monthly networks was highly significantly positively correlated with the network based on all 30 months of data ($r > 0.651$, $P < 0.001$ for all correlations; Appendix L). This suggests that the networks

produced using data collected in one month were reasonable representations of the network based on three years of data.

a)



b)

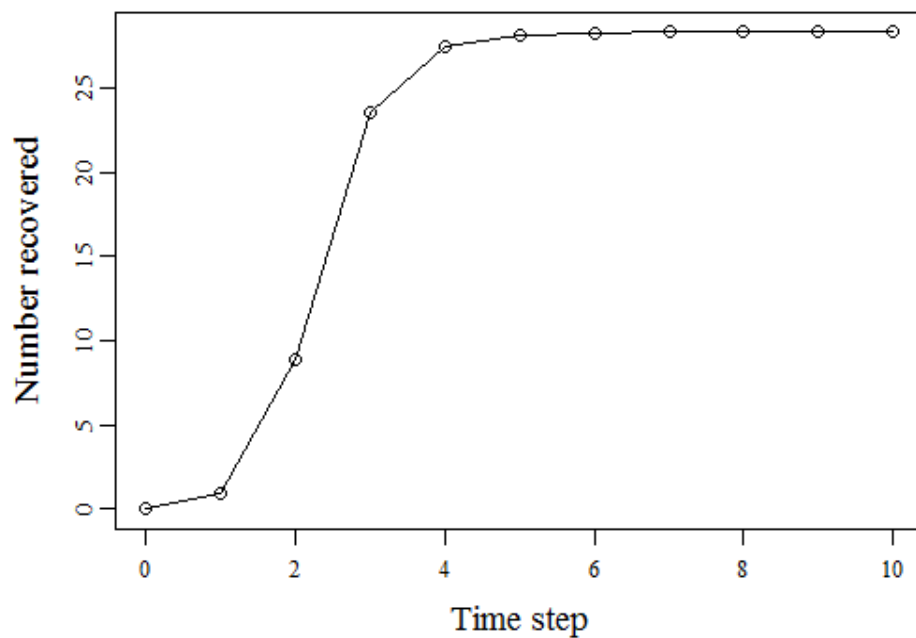


Figure 5.20: The average number of a) infected individuals and b) recovered individuals at each time step ($\beta=1.0$, $\gamma=1.0$) over the 30 networks each based on one month of data.

There was no significant difference between the final size of the epidemic in months in the dry season and those in the wet season, indicating that predicted disease dynamics do not vary significantly between seasons (Figure 5.21: Mann-Whitney U test: $z = -1.594$, $N = 30$, $P = 0.111$).

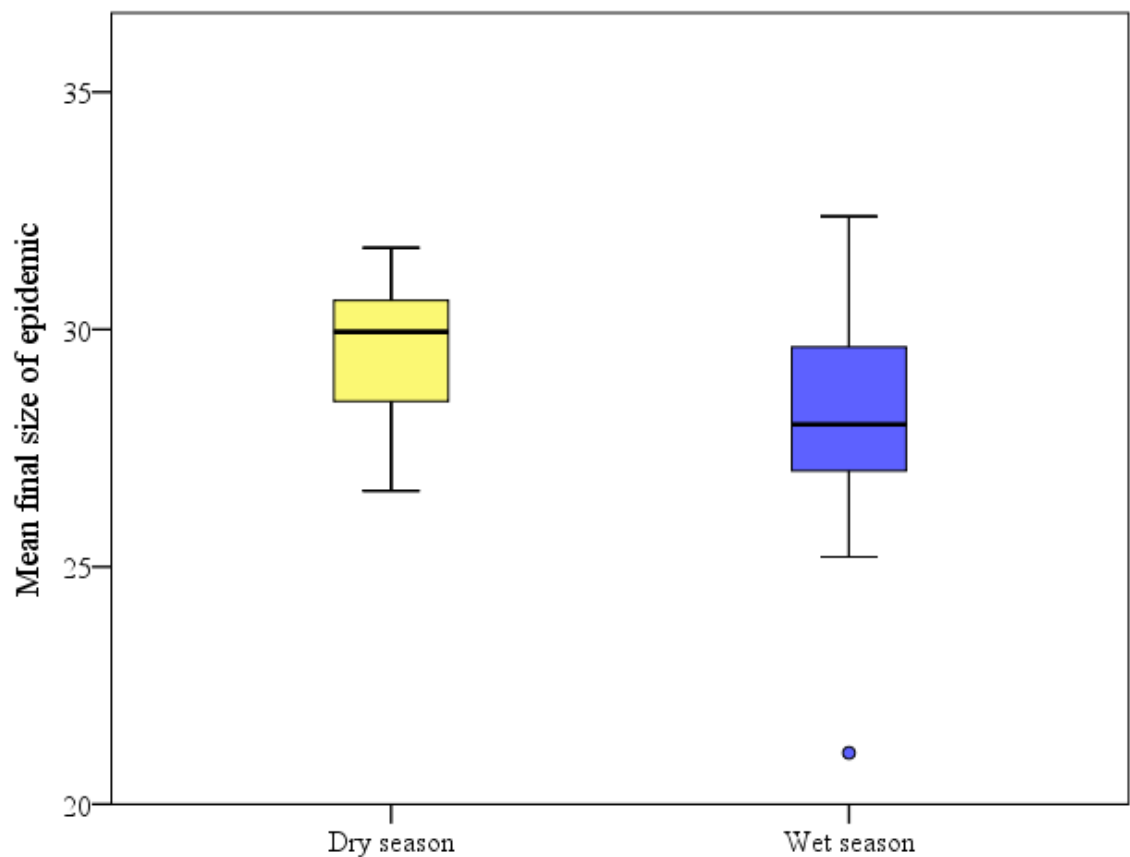


Figure 5.21: Mean final size of the epidemic predicted for months during the dry season and months during the wet season.

5.3.5 The importance of short-term relationships: the orangutan agent based model

5.3.5.1 Validating the model: a comparison with the actual orangutan data

The agent based model was run five times and a number of measures calculated and compared with the observed data to validate the model (Table 5.2). Data were extracted from the models by simulating focal observations on the orangutans and therefore only extracting data from individuals that were being “observed”, mimicking data collection in the real world. All parameters of the agent based model were very similar to the observed values.

Table 5.2: Comparison of behavioural variables extracted from the five agent based model simulations with those observed in reality at Sabangau

Measure	Age/sex class	Orangutan observations	Mean of five simulations of the agent based model
Time spent in association	Unflanged males	27.48	23.39
	Flanged males	3.66	2.71
	Females	21.12	20.14
Mean group size	All	1.20	1.16
Daily distance travelled	Unflanged males	1007	863
	Flanged males	750	833
	Females	798	863
Percentage of time spent feeding on fruit	All	72	76.92
Percentage of time spent feeding on flowers	All	15	16.77
Percentage of time spent feeding on leaves	All	4	6.31

A social network was also extracted from each of the five model runs and network properties compared between these networks and the original network from the observed data (Table 5.3). Almost all measures are similar, although there were some clear differences between the results, with the clustering and assortativity coefficients in particular being higher in the agent based model networks.

Table 5.3: Comparison of mean network properties from the five agent based model simulations with those from the orangutan association network

Network Property	Orangutan observations	Mean of agent based models
Mean degree	7.62	6.01
Mean strength	0.072	0.088
Density	0.21	0.17
Clustering coefficient	0.152	0.466
Mean shortest path length	7.859	8.145
Assortativity coefficient	-0.248	-0.038

The distributions of strength, weighted betweenness, weighted closeness and weighted eigenvector scores were also compared between the actual orangutan data and the agent based models and found to be very similar for all four network properties (Figures 5.22-5.25). The mean values for each of these four network properties for each age/sex class were calculated and compared (Figure 5.26). Again, the results were similar for almost all measures with the exception that the agent based model appears to be somewhat overestimating the strength of unflanged male relationships and underestimating female eigenvector centrality.

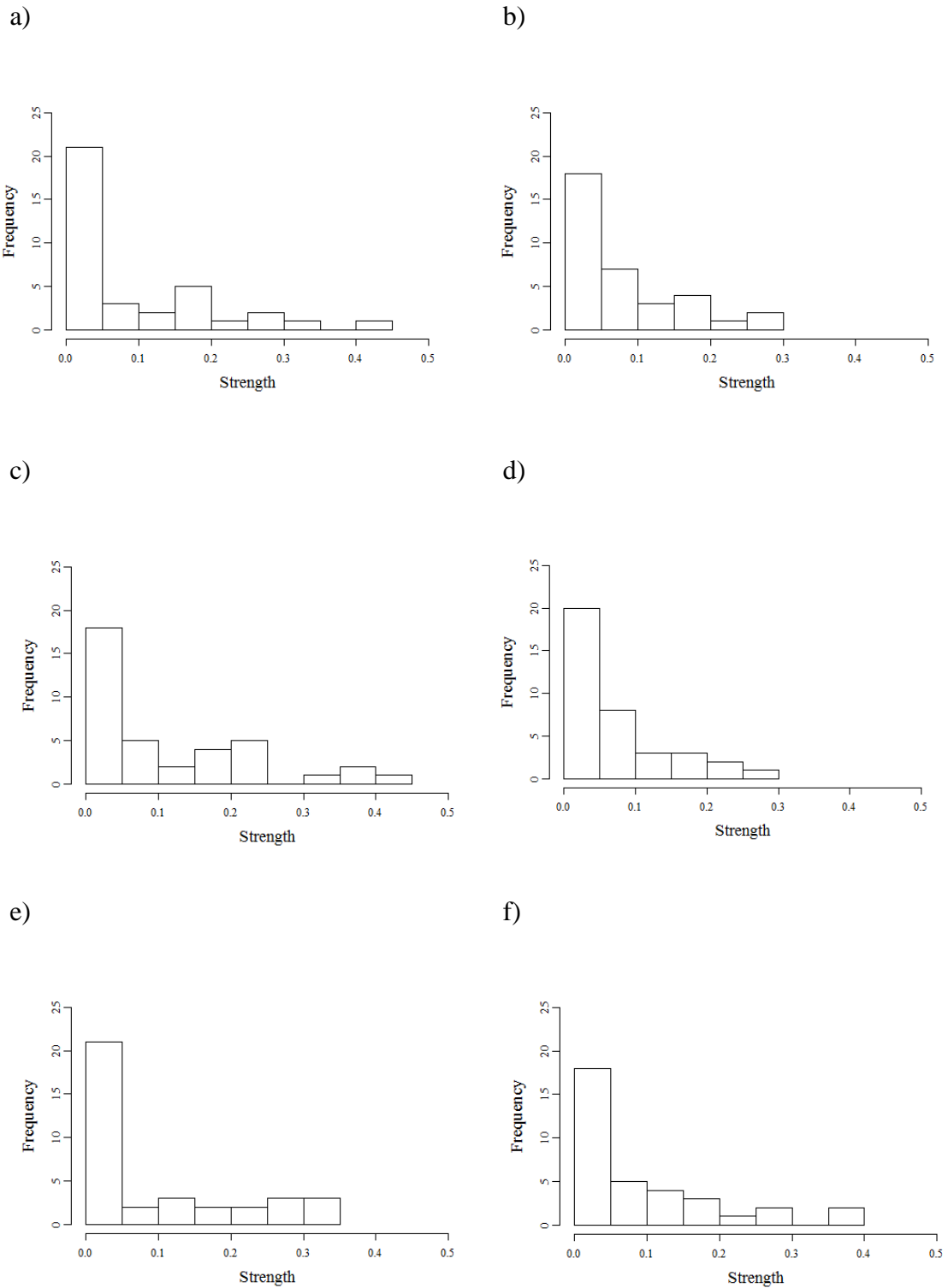
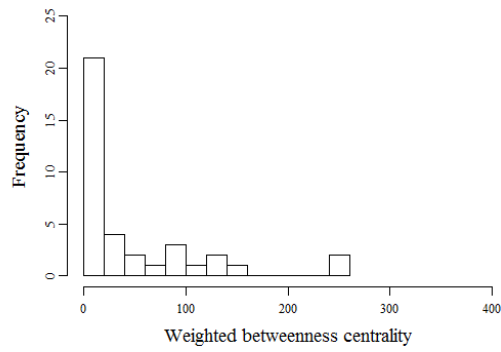
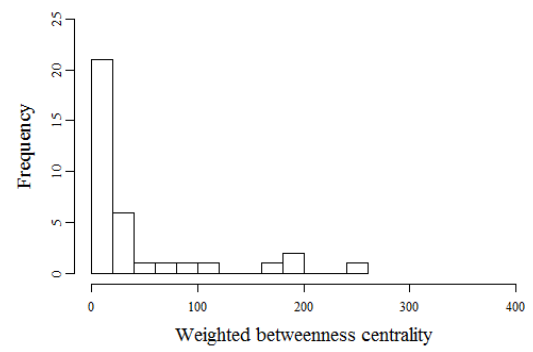


Figure 5.22: Distribution of strength centrality scores in a) the actual orangutan association network, b-f) simulations on the agent based model.

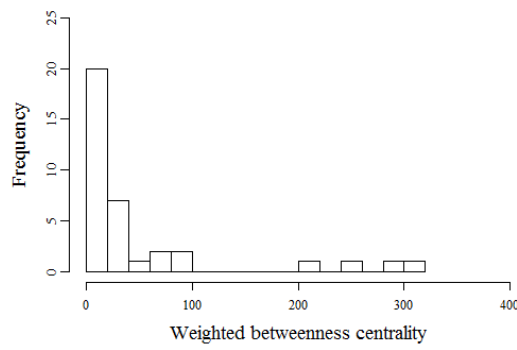
a)



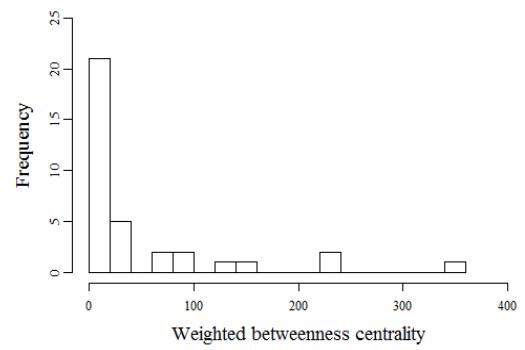
b)



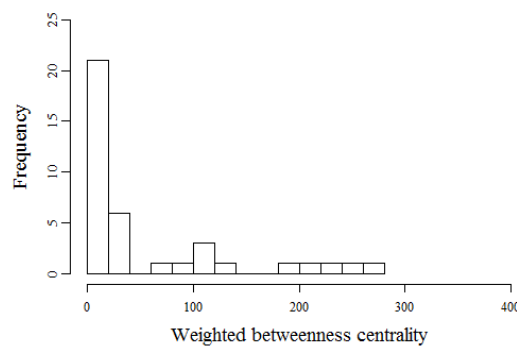
c)



d)



e)



f)

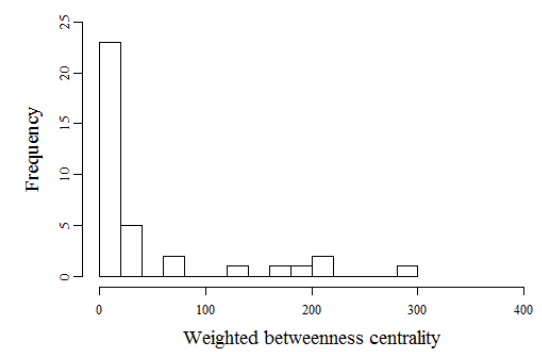


Figure 5.23: Distribution of weighted betweenness centrality scores in a) the actual orangutan association network, b-f) simulations on the agent based model.

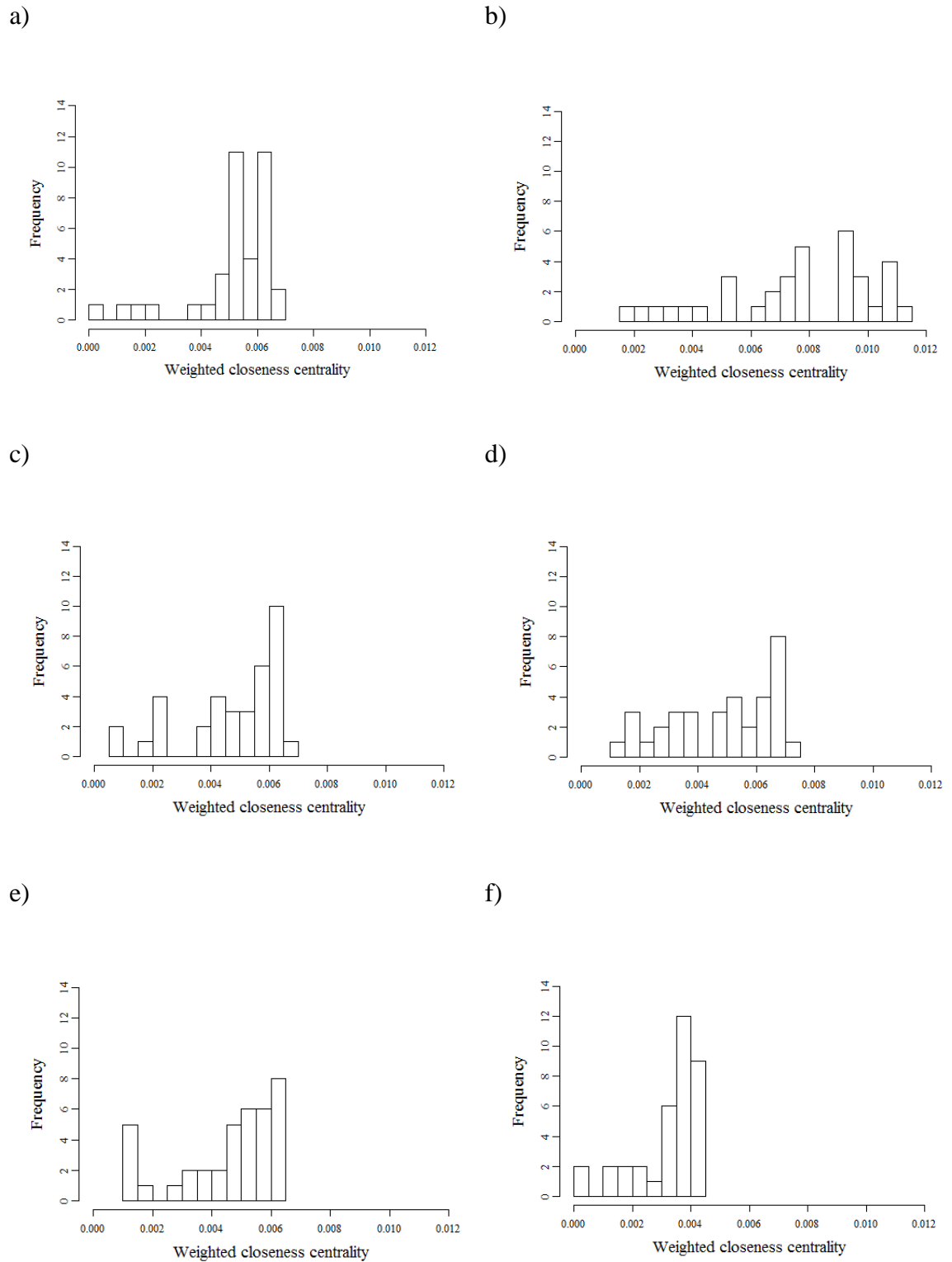


Figure 5.24: Distribution of weighted closeness centrality scores in a) the actual orangutan association network, b-f) simulations on the agent based model.

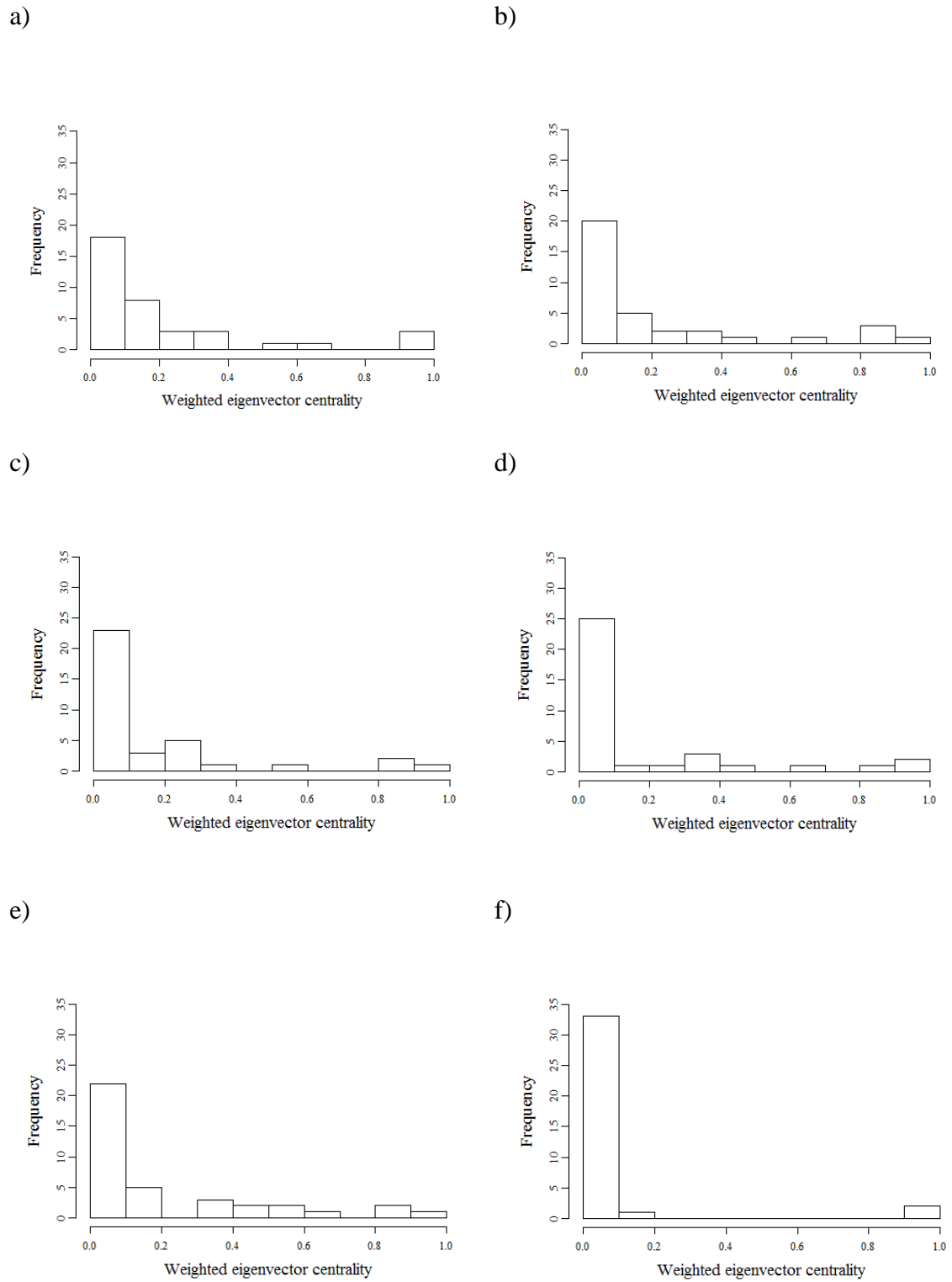


Figure 5.25: Distribution of weighted eigenvector centrality scores in a) the actual orangutan association network, b-f) simulations on the agent based model.

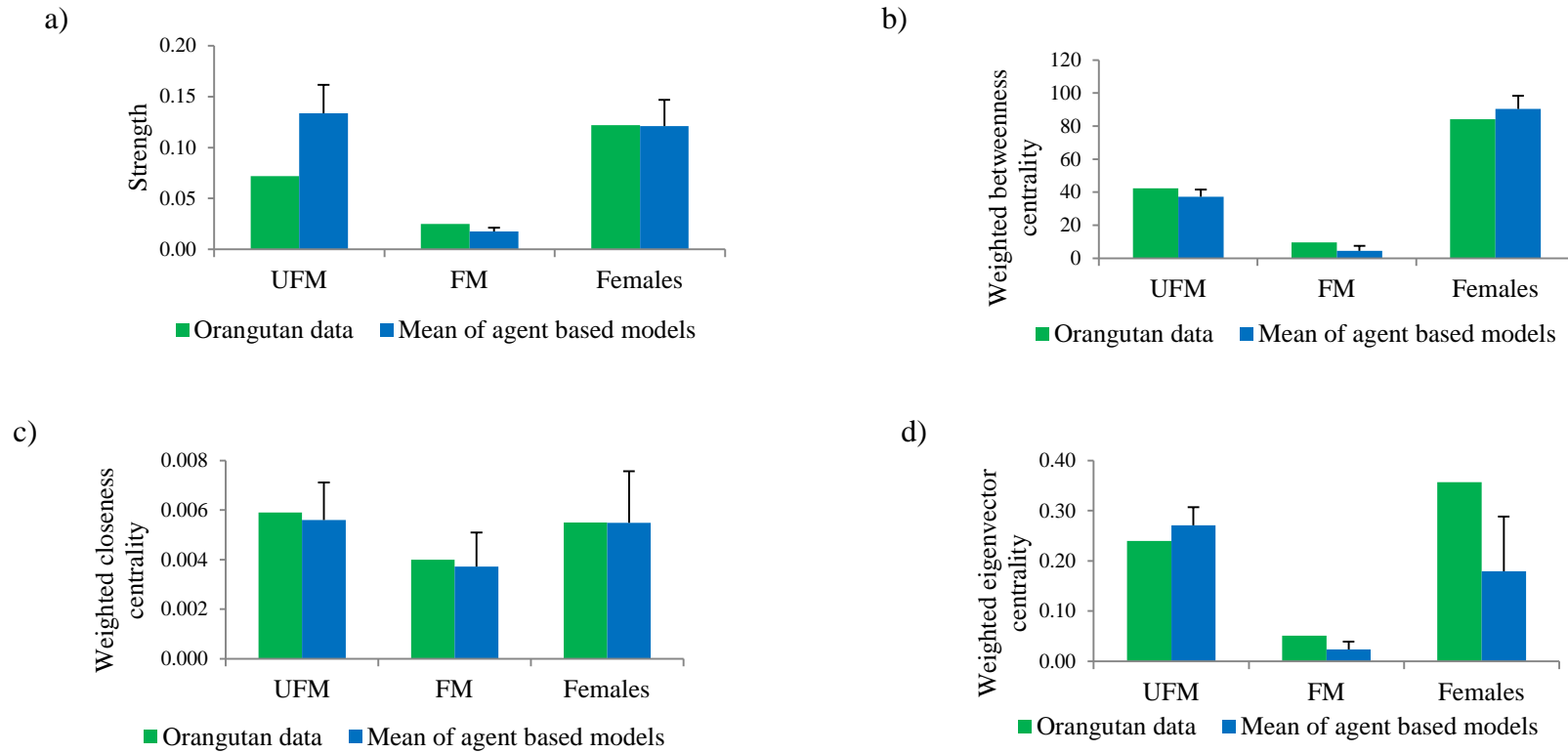


Figure 5.26: Comparison of mean network properties between the network based on actual orangutan data and the mean (+ standard deviation) of the networks based on five runs of the agent based model, where UFM are unflanged males and FM are flanged males.

5.3.5.2 Simulating the spread of disease on the agent based model

The agent based model fit the observed data reasonably well and so was considered an appropriate model of orangutan behaviour. A range of diseases with different transmission and recovery coefficients were simulated on the agent based model for the orangutan (Figures 5.27 and 5.28). Under all combinations of parameters disease failed to spread beyond one individual on average, suggesting that incorporating short-term variation in behaviour does not indicate greater disease spread among orangutans; in fact, the static network model based on nine years of data may overestimate disease spread. Even when the transmission coefficient is ten times greater than the probability of recovery, disease fails to spread.

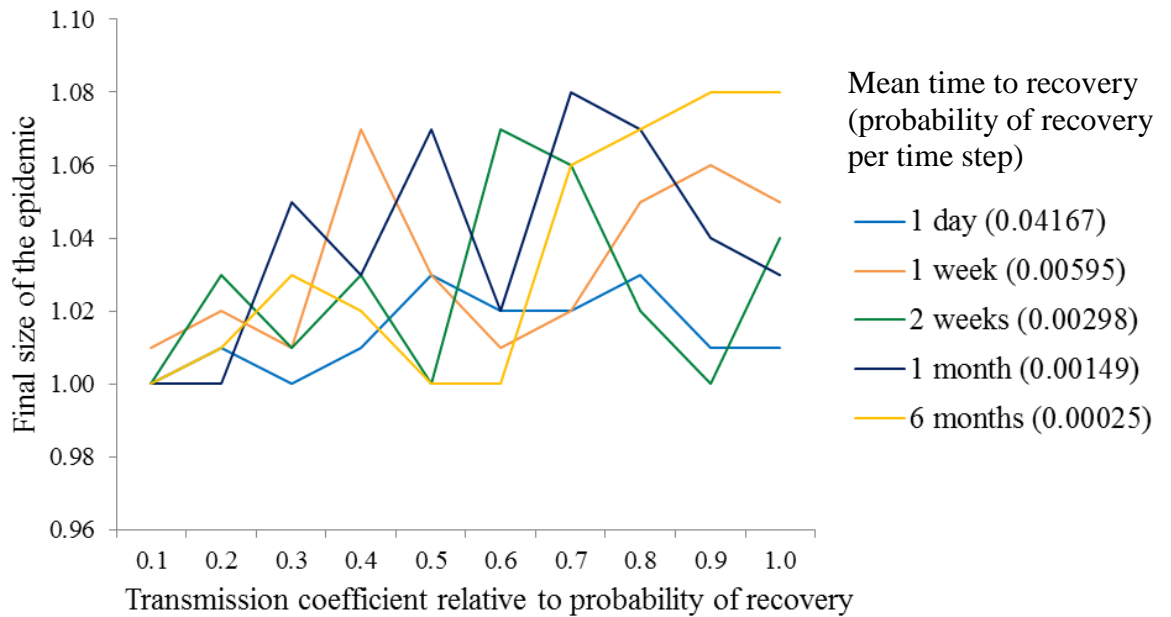


Figure 5.27: The mean final size of the epidemic predicted over 100 simulations of the agent based model for each combination of transmission and recovery coefficient, where the transmission coefficient is less than or equal to the recovery coefficient. For example, where the transmission coefficient relative to the probability of recovery is 0.1, the transmission coefficient is one tenth of the probability of recovery.

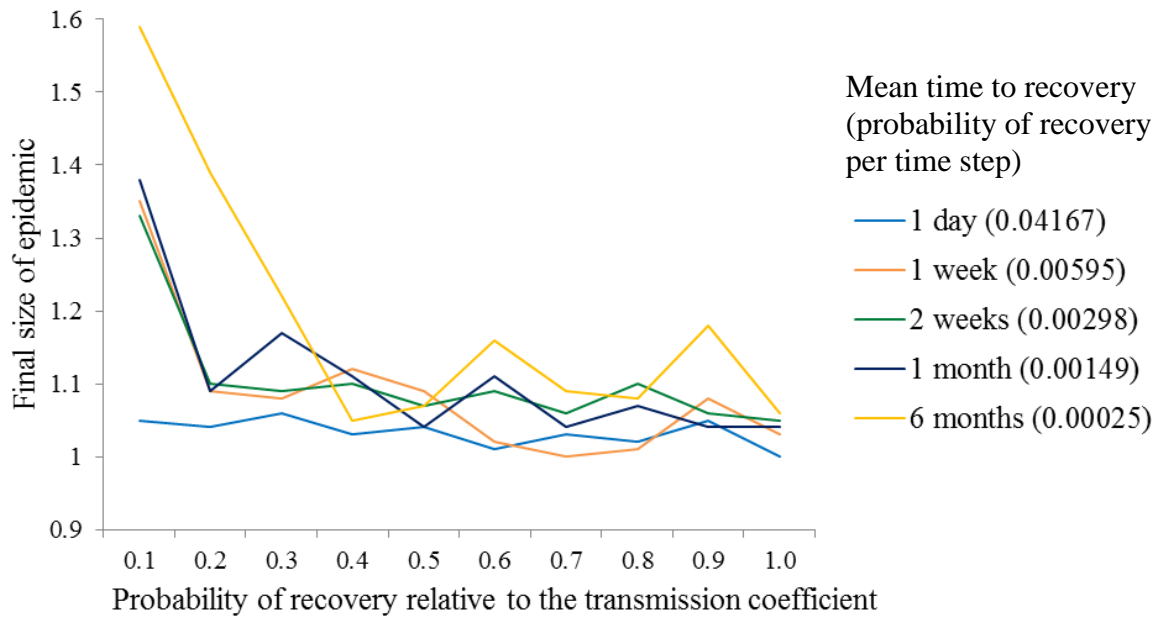


Figure 5.28: The mean final size of the epidemic predicted over 100 simulations of the agent based model for each combination of transmission and recovery coefficient, where the transmission coefficient is greater than or equal to the recovery coefficient. For example, where the probability of recovery relative to the transmission coefficient is 0.1, the transmission coefficient is 10 times the probability of recovery.

5.4 Discussion

Disease transmission was simulated on a network from one population of orangutans based on nine years of association data and a network from one community of chimpanzees based on three years of association data. In comparison to chimpanzees, orangutans appeared relatively robust against the spread of infectious disease. On average, disease did not spread beyond two individuals in the orangutan network. The predictions were very similar using the association, the mean-field and the random networks, suggesting that an association network is not necessary to understand disease spread in this species. In contrast, the chimpanzee network was highly susceptible to disease. The mean field and random networks predicted greater disease spread than the association network, indicating that the inclusion of heterogeneous relationships and the correct topology of the network have important effects on model predictions. The orangutan network was relatively robust against diseases with a range of transmission and recovery parameters, although most susceptible to diseases with a high transmission coefficient and low probability of recovery. Diseases with varying parameters all spread in the chimpanzee network, but those with high transmission coefficients spread to the largest number of individuals. Highly central individuals in both networks were more likely to become infected and more likely to infect others, and the vaccination of these individuals led to a greater reduction in epidemic size than random vaccinations. Both the dynamic chimpanzee model and a model based on the average disease spread in monthly networks supported the prediction that disease would spread rapidly and widely within the chimpanzee community, while an agent based model supported the prediction that disease would not spread between orangutans. Overall, the results

suggest that orangutan populations may be relatively robust against the transmission of infectious disease while chimpanzee communities are highly susceptible to disease spread.

5.4.1 Predicted disease spread among orangutans and chimpanzees

The results of the orangutan static SIR model suggest that orangutan social behaviour makes it very difficult for infectious diseases to spread within the population as a result of the extremely low association indices; disease with certain transmission and recovery at each time step failed to spread beyond two individuals on average, which is only 5% of the network. Disease dynamics across the chimpanzee network were completely different; a disease with the same parameters spread very rapidly and affected an average of 88% of the group. It is clear that disease must be viewed as a serious conservation concern for chimpanzees, while disease transmission between orangutans does not appear to be a major threat. The greater predicted susceptibility of the chimpanzee to disease spread is a result of its greater gregariousness compared to the orangutan, as reflected in the greater number of edges and higher association indices in the chimpanzee network compared to the orangutan network analysed here. Although chimpanzees and orangutans are both characterised by fission-fusion social systems, orangutans spend considerably more time on their own or with only their dependent offspring than do chimpanzees. At Taï, for example, chimpanzees were found to spend on average only 17.6% of the time alone or with their dependent offspring (Lehmann and Boesch 2004), although this increased to 31.7% in a study during the dry season, potentially as a result of greater ecological constraints during this period (Doran 1997). Over the three year study period analysed here, the Sonso chimpanzees spent an average

of 11% of observations alone. Orangutans, by contrast, were shown to spend 81% of their time alone or with dependent infants at Tanjung Puting (Galdikas 1985a) while over 80% of orangutan sightings at Ulu Segama in Borneo consisted of one independent individual (Mackinnon 1974). Similarly, the orangutans in this study were alone for 81% of the time. It is therefore not surprising that disease is predicted to spread more in chimpanzees, as they spend more time with conspecifics and hence there is more opportunity for diseases to spread. Orangutans have been found to have a lower mortality rate than chimpanzees and it has been suggested that this may result from lower risk of disease transmission (Wich et al. 2004). These results provide support for this hypothesis.

The results also support some of the conclusions of the previous chapter; properties of the chimpanzee network suggested that it would be more susceptible than the orangutan network to disease spread as a result of a denser and more strongly connected network. Based on a review of the literature, the only other study of disease transmission in a static network for a wild animal population is that of the killer whales (Guimarães et al. 2007). With transmission and recovery coefficients of 1.0, disease spread to 90% of this population (Guimarães et al. 2007), similar to the chimpanzee network in which 88% of the community were predicted to be infected using the same disease parameters. These killer whales live in small pods with relatively constant membership (on average containing 2.4 individuals, often a mother with her offspring), but pods regularly join to form multi-pod groups (Baird and Whitehead 2000). This social system has evident similarities with that of the chimpanzee, which may explain the similar predictions. It may tentatively be concluded that highly gregarious species with a fission-fusion social system may be very susceptible to disease spread. Fine-grained features of chimpanzee

social structure vary between sites; however, communities from all four subspecies are characterised by a fission-fusion social organisation and, in particular, high levels of gregariousness (Newton-Fisher et al. 2000, Anderson et al. 2002, Morgan and Sanz 2003, Sommer et al. 2004). Other communities of chimpanzees may consequently share a similar susceptibility to disease spread but further studies are required to substantiate this claim. It would be interesting in the future to look at potential disease spread in a gregarious species with more stable social groupings, such as the gorilla, to further evaluate the impact of fission-fusion behaviour on disease spread.

Varying the disease parameters provided further support for the clear differences between the two networks in terms of disease vulnerability. Even diseases with very high infectiousness and very slow recovery did not infect more than five of the 37 orangutans on average. Although it should be emphasised that the loss of five individuals could have an important impact on the population, particularly if they were the central females, a highly infectious disease associated with low recovery is clearly a worst-case scenario. The chimpanzee network, in contrast, was highly susceptible to diseases with a range of parameters, particularly those with medium to high transmission coefficients. This demonstrates that the chimpanzee community is likely to be extremely susceptible to very contagious diseases, for example measles and pertussis (Crowcroft and Pebody 2006). Even diseases with low infectivity and rapid recovery, a best case scenario in terms of disease parameters, spread to a high number of chimpanzees. To date, chimpanzee communities have been affected by a number of diseases and these have been shown to have had dramatic effects on populations as well as individual communities. In the Minkebe forest of Gabon, for example, it has been estimated that Ebola caused the observed 99% decline in chimpanzees (Huijbregts et al.

2003). Over five outbreaks of respiratory diseases at Taï between 1999 and 2006, an average of 92.2% of individuals showed symptoms (Koendgen et al. 2008). A respiratory epidemic within the Sonso community in 1999 affected 23 out of the 34 chimpanzees observed during the course of the outbreak (Reynolds 2005). Chimpanzees are clearly very susceptible to disease spread. The extent of this vulnerability, to diseases varying widely in transmission and recovery parameters, is a serious conservation concern.

The results from these models clearly have a range of implications for future conservation. The resilience of the orangutan network against disease spread has both positive and negative implications for the conservation of the species. The relative lack of disease spread, particularly in comparison to the chimpanzee, suggests that infectious disease is not a major threat to the orangutan. Even if a highly infectious disease with a low recovery rate emerged in the population, most of the individuals are predicted to remain unaffected. This resilience to disease, however, also has disadvantages. The results suggest that the orangutan social system prevents individuals from being regularly affected by infectious disease. This means that over their recent evolutionary history, orangutans may have been exposed to relatively few diseases and may consequently have a very low natural resistance or immunity to infection. Indeed, death rates from disease are high in both zoos and reintroduction centres (Warren 2001) and in zoos orangutans have been observed to be more susceptible than the other great apes to *Strongyloidiasis*, a disease caused by an intestinal parasite (Munson and Montali 1990). Bornean orangutans, the less social species of orangutan in the wild, were found to show signs of chronic respiratory disease significantly more often than Sumatran orangutans in European zoos (Zimmermann et al. 2011). This suggests that there may

even be a difference in disease resistance between the two species of orangutan, that may be linked to differences in sociality and hence exposure to disease over recent evolutionary history. Additional precautions may need to be taken in reintroductions to ensure that diseased animals are not released, and in reintroduction centres to prevent the spreading of disease between rehabilitants. Warren (2001) found that there was a high level of disease transmission between rehabilitants at Wanariset Orangutan Reintroduction Centre, while a respiratory disease was found to spread from rehabilitants to wild individuals at Ketambe (Rijksen 1978). Rodent populations are usually high in rehabilitation settings, which could increase the risks of diseases such as Hantavirus spreading from rodents to orangutans (Chen et al. 2011), especially as rehabilitants usually spend far more time on the ground than wild orangutans (Russon 2009). An increase in terrestriality may also lead to greater contact with potentially infected faeces. If orangutans have a low resistance against diseases, orangutan rehabilitants need to be closely monitored for disease to improve the survival rate of animals for reintroductions.

The rise of ecotourism is also a concern for the conservation of the orangutan, at least in terms of potential disease transmission. A significant proportion of tourists visiting Sepilok Orangutan Rehabilitation Centre were ill and potentially infectious (Muehlenbein et al. 2010). Parasite prevalence in orangutans was shown to be higher at Bukit Lawang, a site where tourists are permitted and orangutans spend more time on the ground and interacting with each other than at Ketambe (Foitová et al. 2009). With the pressures of human encroachment that are set to increase in the future, the risk of disease transmission from humans is likely to increase and deforestation may force orangutans to live at higher population densities in the remaining fragments of forest.

This could potentially lead to a social system more similar to that of the chimpanzee and thus lead to increased opportunities for disease spread. If orangutans have indeed had a limited exposure to disease, these pressures may have considerable negative effects on the survival of the species.

In contrast to orangutans, chimpanzee social structure makes chimpanzees very susceptible to infectious diseases. Infectious disease is predicted to be able to spread extremely quickly to a large proportion of community members. This is a worrying finding as chimpanzees will have little natural immunity to diseases derived from humans or to newly emerging diseases. Ecotourism and research are therefore predicted to be serious threats for this species. The spread of diseases from humans has already been implicated in a number of epidemics in chimpanzees (Kaur et al. 2008, Pusey et al. 2008) and mortality from disease is often high (Williams et al. 2008). Ecotourism has many associated benefits, such as providing finances and local support for the conservation of great apes (Homsy 1999), and so it is not practical to recommend the complete cessation of great ape tourism. However, the rapidity with which diseases can spread between chimpanzees is a clear warning that hygienic measures must be strictly enforced to prevent the introduction of disease into the chimpanzee communities. Regulations have been widely introduced at great ape tourism sites to reduce the impact of visitors, particularly in terms of disease transmission (Macfie and Williamson 2010). These often include a minimum distance that visitors have to maintain between themselves and the apes, wearing face masks, burying or removing all human waste and the prevention of tourists with visible signs of infection from visiting the apes (Homsy 1999, Macfie and Williamson 2010). At a number of sites these measures appear to have had a positive impact in preventing death from respiratory disease (Lukasik-Braum

and Spelman 2008). However, the regulations are often difficult to enforce and hence often broken. Tourists are regularly ill at the time of the visit (Adams et al. 2001, Muehlenbein et al. 2010) or get closer to the apes than regulations allow (Sandbrook and Semple 2006). The number of groups or individuals allowed to visit a chimpanzee community each day is often exceeded (Nakamura and Nishida 2009). It is going to be vital for the future survival of the chimpanzees involved in all ecotourism initiatives that these rules and recommendations are more strictly adhered to and enforced, because when a disease is introduced it will be very difficult to prevent it from spreading, and the slow life histories mean that populations will take many years to recover.

In addition, disease transmission from local people and park staff may be a considerable risk. At Kibale, for example, gastrointestinal bacteria from chimpanzees were more similar genetically to those from humans working in research and tourism than those from the inhabitants of a local village (Goldberg et al. 2007), suggesting some level of transmission of bacteria between chimpanzees and tourists/research workers. Current recommendations include a need to vaccinate park staff and the improvement of the health care available to the local people (Homsy 1999). The results presented in this chapter provide further support for the importance of these measures, as the spread of disease from local people and park staff to the chimpanzees could have dramatic effects on population size. A disease prevention strategy is therefore expected to be the most successful solution.

It is important, however, to consider the limitations of this study when interpreting the results. Firstly, the definition of social contact employed has an important influence on the applicability of the results. Both orangutans and chimpanzees were said to be

associating if they were within 50 metres of one another (Morrogh-Bernard 2009, Zuberbühler, personal communication). Although for much of the measured association time individuals will in fact be in much closer proximity than the 50 metre cut-off distance, many diseases require very close contact for transmission (Homsy 1999), for example sexually transmitted diseases and those caused by parasites, which are also further complicated by stages of the life cycle spent outside the host and the number of parasites infecting each host (Anderson and May 1991, Nunn and Altizer 2006). In addition, many diseases are spread through the faecal-oral route where the link between association and transmission is less clear; for example, viruses causing diseases such as polio can survive for several months in the soil (Homsy 1999) and so may be transmitted between individuals that have never been in proximity. In some cases, using contact networks instead of association networks might be more appropriate, and similar models to those used here could be run on these other types of networks. This would likely lead to lower predictions of disease spread in both species. The results do, however, provide a general model of the spread of respiratory diseases, which are both relatively common and extremely threatening to great apes (Pusey et al. 2008, Williams et al. 2008). Improving our understanding of the spread of respiratory disease is important for these species, especially in regards to the appropriate management of both research and ecotourism sites.

A related limitation is the extent to which the largely theoretical results in this chapter can be translated into predictions for actual diseases. Very little is known about the specific parameters of the diseases that affect great apes, such as the proximity and duration of contact required for transmission or the infectious period of particular respiratory diseases. The results in this chapter therefore cannot be used to predict the

mortality rates that a specific disease would cause. However, the results do provide a general estimation of the susceptibility of orangutans and chimpanzees to the spread of diseases with differing characteristics representing worst and best case scenarios.

5.4.2 The importance of association data for disease predictions

The mean-field and the random networks produced almost identical results to those from the actual orangutan association network. In terms of the mean-field model, this indicates that using a simple average of the amount of time orangutans spend in parties would be enough information from which to model disease spread. In terms of the random network, this indicates that the fine-grained structure of the orangutan network has no real impact on disease spread; the orangutans are no more or less susceptible to disease than they would be if association partners were selected at random. This is an unusual result in comparison to previous studies on other species in which mean-field models were shown to estimate higher disease spread than did network models (Eames and Keeling 2002, Cross et al. 2004, Duncan et al. 2012). Killer whale networks based on detailed association data were shown to be more susceptible to disease than equivalent random networks (Guimarães et al. 2007). It seems likely that the extremely low association indices between orangutans in the network prevent the spread of disease, regardless of the topology of the network.

Although the orangutan results are based on data from only one population, it seems likely that they are more widely applicable, at least to other populations of Bornean orangutans. The orangutans in this study were found to spend around 81% of their time alone, which is comparable to values found at Tanjung Puting (Galdikas 1985a) and Ulu Segama in Borneo as well as Ranun in Sumatra (Mackinnon 1974). The similarity in the

predictions from the association network, the mean-field model and the random model suggest that it is the low levels of association rather than the structure of the orangutan society that leads to this pattern. It therefore seems reasonable to conclude that other populations of orangutans and perhaps even other species with comparable low levels of sociality will be characterised by similar predictions of disease dynamics. However, not all populations of orangutans have such low levels of association; for example, average party size has been shown to be higher at a number of sites in Sumatra than those in Borneo (van Schaik 1999). Disease may consequently spread to slightly more individuals in a population of Sumatran orangutans. It would be interesting to run the analyses on data from a Sumatran population to determine if the outcomes of the model support this idea.

In contrast, the results of the mean field and the random networks for the chimpanzee models provide support for the importance of using an association network approach in disease simulations for this species. Incorporating heterogeneity in relationships appears important to gain a reliable understanding of disease dynamics in the chimpanzee, and to prevent overestimation of epidemic sizes and speed. It is likely that there is a threshold level of association above which it becomes useful to incorporate dyadic association data. Without data from a wider variety of social systems it is difficult to estimate where this threshold may lie; however, it is clear that for highly gregarious species such as chimpanzees, the inclusion of association data can have important effects on predictions.

5.4.3 *The importance of superspreaders on disease dynamics*

The presence of superspreaders in a group or population can have an important effect on the speed and pattern of disease spread. Properties of the association networks and the results of removal simulations performed in the previous chapter suggested that there may be superspreaders in the orangutan network but not in the chimpanzee network. This was investigated in more detail using the SIR models, to provide more in-depth predictions of the effect that potential superspreaders could have on disease spread. Interestingly, in both species, individual centrality had a clear impact on the ability to transmit disease and the risk of becoming infected. Although the relationships were not all linear, almost all of the centrality measures tested were strongly positively associated with both the mean number of secondary infections caused and individual disease risk. The only exception was weighted betweenness in the chimpanzee network, which had no significant relationship with either measure. Nevertheless, individuals with high weighted betweenness centrality do still cause a high number of secondary infections and have a high infection risk. A number of other studies on a range of network structures have found similar positive correlations between centrality and the number of secondary infections caused (cocaine injectors, Bell et al. 1999; Italian cattle movements, Natale et al. 2009; theoretical networks and a network of US air transport, da Silva et al. 2012) and between centrality and infection risk (cocaine injectors, Bell et al. 1999; theoretical networks, Christley et al. 2005; human physical contacts, Eames et al. 2009). Consequently, this is likely to be a common pattern in disease spread.

However, although the positive relationship holds in both orangutans and chimpanzees, more careful consideration of the results highlights important differences between the

two. In the orangutan network, the majority of individuals are concentrated at the lower end of the graph, with low centrality and minimal secondary infections and infection risk. The distribution of points on the chimpanzee plots is completely different; most individuals are concentrated at the higher end of the graph. This means that in the chimpanzee community there are a large number of individuals with the ability to spread disease widely and with high risk of infection, while in the orangutan network, two or three individuals have much higher scores relative to the rest of the population. Superspreaders are defined as individuals that cause an unusually large number of secondary infections (Lloyd-Smith et al. 2005). In the chimpanzee network lots of individuals cause a large number of secondary infections, but because of the high number of them, this is not unusual. In contrast, in the orangutan network three individuals cause unusually high numbers of secondary infections compared to the others in the network, but in absolute terms, these individuals in fact have a very limited ability to spread disease. It can therefore be concluded that superspreaders do not in fact exist in either network, as in each case only one of the two requirements is fulfilled. This implies that a simple analysis of the distribution of network metrics may not be sufficient to identify superspreaders as it does not take into account the absolute number of infections caused.

The importance of potential superspreaders was investigated further by simulating the spread of disease following the vaccination of central and random individuals. Again, this expands on the removal analyses in the previous chapter by producing predictions about the reductions in disease spread following vaccinations as opposed to simply the impacts on network cohesion. Vaccinations, both random and targeted, reduced the final size of the epidemic under all of the different strategies in both species, as expected. For

both networks, targeting individuals with high centrality was more effective in reducing the final size of the epidemic than targeting individuals randomly. Similar results have been found in scale-free networks (Pastor-Satorras and Vespignani 2002, Bai et al. 2007), small-world networks (Zanette and Kuperman 2002) and a human physical interaction network (Eames et al. 2009); therefore targeting central individuals may be a widely applicable vaccination strategy. Interestingly, targeting individuals based on high binary centrality produced a similar reduction in epidemic size to targeting individuals with high weighted centrality in both orangutan and chimpanzee networks. This suggests that even a simple measure such as the number of contacts each individual has can be used to create an effective targeted vaccination campaign.

The orangutan results, however, suggest that for this species a vaccination programme is unlikely to be needed. Although both forms of vaccination strategy reduced disease spread, the amount of transmission was already very low and so this reduction is very minor. It seems likely that the disadvantages in terms of the cost, stress to the animals and the possibility of the vaccine actually resulting in disease (Cabezas et al. 2006, Blancou et al. 2009), would outweigh the benefits achieved through the small reduction in disease spread. In addition, although the relative difference between targeted and random vaccinations is considerable, in absolute terms, this difference is minor. Consequently, in terms of absolute effects on population size, targeted and random vaccinations would have a similarly small effect. This links back to the finding that superspreaders do not in fact exist in the orangutan network, as despite the skewed degree distribution, none of the orangutans have the ability to infect a large number of network members. Vaccinations are not predicted to be a very effective method of reducing disease spread in orangutans, simply because disease never spreads very far.

In contrast, the chimpanzee community is extremely susceptible to disease and both targeted and random vaccinations led to quite large absolute reductions in epidemic size, at least in comparison to the orangutan network. However, even after the vaccination of 20% of the community, an epidemic can still affect 67% of the community when vaccinations are random and 64% when they are targeted (for a disease with a transmission and recovery coefficient of 1.0). These results are similar to those from a killer whale network, in which randomly assigning 20% of individuals to a non-susceptible class still led to epidemics affecting over 50% of the group (Guimarães et al. 2007). Vaccinations therefore did not lead to widespread immunity in the chimpanzee community and were not predicted to be very effective in protecting non-vaccinated individuals. This is a result of the high number of redundant links between individuals, meaning that even following a high number of vaccinations there are still multiple potential disease pathways between individuals. At least 60% of the community would therefore need to be immunized to prevent a disease from spreading. In gregarious species such as these it may be more important to focus on disease prevention than response as once a disease has invaded a population the predictions suggest that it will be very difficult to stop.

It is also important to note that although targeted vaccinations are more effective than random vaccinations in the chimpanzee network this effect is not strong at low vaccination levels. If identifying or finding specific individuals to target is heavily time and resource consuming, random vaccinations may be a preferable strategy, especially if overall vaccination rates will be low as a result of limited resources. In terms of selecting a measure with which to identify central individuals to target, weighted betweenness centrality was the least reliable measure. This is interesting in relation to

the results from Chapter 4, which indicated that weighted betweenness was the most positively skewed metric, and that fragmentation was the greatest following the removal of individuals with high weighted betweenness. However, this simulation consisted of removing only 20 individuals, and in fact choosing weighted betweenness for the first 20 vaccinations leads to results similar to the other metrics. After the first 20 individuals, however, most of the individuals in the network have the same very low betweenness centrality and so removal is essentially random (where individuals have the same value the selection is alphabetical). This explains why the vaccination of these individuals has a similar effect to random vaccinations.

The other three centrality metrics generally performed equally well. Individuals with high centrality under one measure usually had high centrality for all measures, and so it is not surprising that the predictions were similar for these three metrics. The most efficient strategy would therefore be to target individuals using the centrality measure that requires the least effort to calculate; probably an individual's degree or strength. However, unless a large number of chimpanzees can be targeted, vaccination is not predicted to be a very efficient or effective disease prevention measure.

5.4.4 The chimpanzee dynamic model

The predictions of the dynamic model were similar to those from the static model, although predicting lower overall disease spread. This suggests that the use of a static network provides a fairly good approximation of disease spread in chimpanzees (assuming that using dynamic networks is a more accurate representation of the structure of the chimpanzee society). Similarly, when a model of foot-and-mouth disease was run on a network of livestock movements, both static and dynamic models

produced similar results (Kao et al. 2006). Volz and Meyers (2009) created a neighbour-exchange model in which relationships were rewired over time according to a fixed rate. This rate of change was varied and the results compared with equivalent static models. Static models were found to be an adequate approximation of the dynamic results when the rate of rewiring was low or medium, but not at high rates. It could be inferred from this finding that the similarity between the predictions of the chimpanzee static and dynamic models is a result of a low rate of change in relationships. Chimpanzees have been shown to have many long-term social bonds, often lasting for months or even years (Gomes et al. 2009, Lehmann and Boesch 2009, Mitani 2009). The rate of change in relationships between monthly networks may consequently be quite low, leading to relatively similar predictions between the two types of model. This is supported by the generally high correlations of each of the monthly networks with the overall network based on all of the data.

However, it is important to recognise that although the models produce relatively similar predictions, there are still clear differences between the two. For example, the chimpanzee static model tended to predict a larger final epidemic size than the dynamic model. A number of previous studies have found similar results when comparing static and dynamic simulations. Fefferman & Ng (2007) compared static and dynamic models using a theoretical association network and found that disease incidence was higher in the static than the dynamic model. A study of cattle movement networks in the UK showed that the weighted static network consistently failed to match the predictions of the dynamic models by considerably overestimating disease spread, particularly when transmission coefficients were high (Vernon and Keeling 2009). Interestingly, increasing transmission coefficients also led to a greater discrepancy between the results

of the chimpanzee static and dynamic models. At low transmission coefficients the dynamic model actually predicted greater disease spread, while at high transmission coefficients the static model predicted much larger epidemics. This is because at high transmission coefficients, disease spread in the dynamic network is limited by the temporal variability in the presence of connections. In contrast, in static networks all links are permanent and so disease spread is instead limited by the transmission coefficient (Vernon and Keeling 2009). When the transmission coefficient is high, disease can spread considerably more in the static network. It is interesting that at low transmission coefficients the dynamic model predicts greater disease spread; this may be an indication that the strength of relationships in the dynamic networks is greater than that in the static network. This suggests that although the static model appears to be a reasonably accurate approximation of the dynamic results, this is only the case for diseases with low to medium transmission coefficients; for diseases with high transmission coefficients the static model may overestimate disease spread. The fact that at very low transmission coefficients, the static model may underestimate disease spread may have important implications for conservation. If a model underestimates disease spread this could lead to insufficient action being taken to prevent an epidemic, which could have disastrous effects on survival rates. The results of these models should therefore always be treated with an appropriate level of caution. It should also be emphasised that although the dynamic model was based on data at a higher temporal resolution than the static model, this could still be improved. For a truly accurate model of potential disease spread, networks would need to be based on all interactions that occur and not just those that were sampled. The huge amount of data that would be required for this is not practical, and so the dynamic model can be considered to be a

more realistic alternative. The fact that the results from the dynamic model support the conclusions drawn from the static model, that chimpanzees are highly vulnerable to disease outbreaks, provides confidence in this finding.

5.4.5 The spread of disease on monthly chimpanzee static networks

In order to investigate the dynamics of diseases that spread over a time period shorter than one month, an SIR model was simulated on each of the months of chimpanzee data in turn. Although the overall static network can be used to investigate diseases at this time frame, as it is assumed to represent the overall structure of the society, it includes all relationships that occur over the whole three year period and may consequently overestimate disease spread at shorter time frames. The monthly networks predicted on average a much smaller epidemic (of 28 ± 2 individuals) than the 47 chimpanzees infected under the static model. This could be interpreted as an indication that diseases that spread over a shorter time scale will infect fewer individuals and that it is therefore important to analyse data at the time scale at which the disease spreads in order to make robust conclusions (Craft and Caillaud 2011). Alternatively, it could be that the data available from one month of data collection is not sufficient to reflect the true association network accurately, particularly for a fission-fusion species. The chimpanzee social organisation means that typically at any one time the community is separated into numerous subgroups (Reynolds 2005). It is therefore very difficult to record associations for all group members at once. Consequently, focal follows are performed on each individual in order to gain an overall representation of their social interactions (Altmann 1974). It is possible that longer term data, or more intensive observation effort, are required to form robust conclusions about social structure (Croft

et al. 2008, Perreault 2010). Limited observation effort may lead to relationships, i.e. potential disease pathways between individuals, being missed. The result will be a network with fewer disease pathways and consequently a smaller predicted epidemic. However, there was no significant relationship between observation effort and the predicted size of the epidemic across the monthly chimpanzee networks. In addition, observation effort was not significantly correlated with the number of individuals or relationships observed. Overall, this suggests that the smaller epidemic size predicted in the monthly networks should not be attributed to insufficient observation effort. Instead, it seems that the lower number of relationships observed during one month is an accurate reflection of chimpanzee sociality.

Chimpanzees live in quite large communities, but spend the majority of their time either alone or in small parties that regularly change in composition (Mitani et al. 2002). Chimpanzees have been found to express clear preferences in association partners that can last over many years (Watts and Mitani 2001, Lehmann and Boesch 2009), but also form more temporary relationships to satisfy current needs (Mitani 2009). Temporary partners will therefore change over time; for example, coalitions between male chimpanzees can be relatively flexible, changing in order to maximise social status (Nishida 1983, de Waal 1984, Gilby and Wrangham 2008), while females become considerably more gregarious when in oestrus (Pepper et al. 1999). Party sizes have also been found to decrease during periods of low food availability (Chapman et al. 1995, Wrangham 2000, Anderson et al. 2002), meaning that there will be fewer dyadic relationships observed. Finally, community membership also changes over time, as individuals die, emigrate or immigrate. This means that during any particular month chimpanzees are not likely to associate with all of the partners they are observed with

over the three years. It therefore seems probable that the predictions based on the monthly networks are accurate estimates of the spread of disease over a shorter term. This finding has interesting conservation implications, as it suggests that diseases that spread over a shorter time scale, such as measles or influenza, may infect fewer chimpanzees overall than those that spread more slowly, such as tuberculosis.

Although the monthly networks did contain fewer dyadic relationships than the overall 30 month network, they were all still highly correlated with the 30 month network, indicating that they are a reasonable approximation of the overall network structure. This is interesting in terms of data collection as it implies that extensive periods of fieldwork are not required to gain an insight into chimpanzee network structure. The lack of a correlation between observation effort and in particular the number of edges in the networks provides further support for this statement. Data collected over a period as short as a month may consequently be sufficient to gain an understanding of the network structure of this community of chimpanzees. The correlations between the monthly and the overall network also indicate a high level of stability in the chimpanzee social structure between months. At Budongo party size was shown to have a negative or no relationship with food availability and little association with food dispersion (Newton-Fisher et al. 2000). It was suggested that this was a result of generally high food abundance throughout the year (Newton-Fisher et al. 2000). A constant level of high food abundance at Budongo may lead to the social structure remaining relatively constant throughout the year.

There was no significant difference between the predicted final size of the epidemic between the months during the dry season and those in the wet season. This differs from

a study of African buffalo which were shown to be more vulnerable to disease spread in the dry season than the wet season, as a result of increased clustering during dry conditions (Cross et al. 2004). Previous field studies of chimpanzees have found that prevalence of gastrointestinal parasites does vary seasonally, being more prevalent in the dry season at Kibale (Masi et al. 2012) and in the wet season at Mahale (Huffman et al. 1997). However, social structure at other chimpanzee sites may also vary more between seasons. Chimpanzees at Tai, for example, spent considerably more time alone during the dry season (Doran 1997) while at Mahale, chimpanzees formed smaller parties during the late wet season than during the rest of the year (Matsumoto-Oda 2002). Correlations between season and parasite prevalence may also be attributed to direct effects of the climate on parasite abundance rather than indirect effects through changes in social structure. At Mahale, a number of respiratory outbreaks occurred during the dry season, but as this is also the peak tourist season it may not be related to climate (Kaur et al. 2008).

5.4.6 The orangutan agent based model

Overall, the agent based model produced a good representation of actual orangutan social behaviour. There were, however, some key differences between the agent based model results and the actual orangutan network that may have implications for disease transmission and so are important to discuss. Firstly, overall sociality was lower in the agent based model; mean group size and time spent in association for all age/sex classes were lower in the model than in reality, while degree and density were lower in the networks based on the agent based model than that based on actual data. In addition, the clustering and assortativity coefficients were higher in the agent based model networks

than in reality. It is likely that all of these differences relate to the allocation of distinct territories to all individuals. Orangutan populations in fact contain many transient individuals which simply pass through the area, remaining for only a few months, and so it is unlikely that they have clearly defined territories as described in the model. The allocation of territories meant that each individual had a maximum number of orangutans with which it could come into contact (i.e. the number of other orangutans with which its territory overlapped). This may have contributed to the low degree and the generally lower levels of sociality, particularly as individuals classed as rare were given home ranges at the edges of the area and so only overlapped with a very limited number of other orangutans. In addition, as social relationships were more constrained geographically, this may have led to the higher clustering coefficient and less disassortativity (additional relationships between residents who generally have higher strength and rare individuals who generally have lower strength due to fewer opportunities to associate would increase disassortativity in the network). It would be interesting to include an additional class of transient animals in future models that follow different rules regarding ranging patterns, to determine if this improves the similarity between the model results and reality.

The other major difference between the actual orangutan network and those based on the agent based model was in mean strength; this was higher in the agent based model networks than in the actual network. This may also be linked to the distribution of territories, as instead of coming into contact with a range of individuals for a short time, animals repeatedly come into contact with the same few individuals. As observation time for a number of the individuals was extremely low, even a small number of repeated interactions can very quickly lead to very high strength scores. In particular,

unflanged males had much higher strength scores in the agent based model networks and in fact eight of the 16 unflanged males were rare individuals and so likely to be more transient in reality than represented in the networks. In contrast, only four of the 14 females and five of the 16 flanged males were rare.

Overall, there was also a lot of variation in results between the model runs. This was due to the extremely low numbers of observations of many of the individuals, leading to a large element of stochasticity in the results. This in itself is an interesting finding, suggesting that perhaps much of the data collected on individual orangutans is not sufficient to provide a clear indication of their social behaviour. Indeed, extracting data on all associations that occur over the nine year agent based model simulation leads to a somewhat different network (denser, with a higher mean degree but lower mean strength) to that produced by simulating focal observations (personal observation).

Despite these differences, overall the agent based model appears to provide a reasonably accurate representation of the general patterns of orangutan social behaviour. If anything, many of the differences that exist (i.e higher mean strength and greater clustering) are likely to lead to the agent based model overestimating disease spread. However, simulations showed that again disease failed to spread considerably between orangutans, and in fact disease spread even less in the agent based model than on the association network. This suggests that perhaps by including all relationships observed over a nine year period, the network approach marginally overestimates potential disease spread. Disease transmission between wild orangutans appears not to be a major threat to the species.

5.4.7 Implications for the transmission of social information

The results in this chapter provide useful insights into the transmission of social information in both chimpanzees and orangutans. Although the models described here deal with the transmission of disease, there are evident similarities between this and the transmission of social information. Both forms of transmission require some level of association, with the probability of transfer increasing as time in association increases. As a result, the transmission of social information has often been modelled using the equivalent of the Susceptible-Infected network models in epidemiology; studies of both artificial and real primate networks, for example, showed that the structure of the network had a considerable impact on the flow of information (Voelkl and Nöe 2008, Voelkl and Noë 2010). This can be expanded to look at the presence of traditions within groups and populations. Traditions can be defined as ‘enduring behaviour patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group’ (Fragaszy and Perry 2004, p. 3). The classification of a behaviour as a tradition is therefore dependent on its being spread via social interactions. Hence, using a network based disease model, in which disease spreads in accordance with the strength of associations, may provide interesting insights into both the way in which social information can be transmitted and also ultimately the prevalence of traditions.

The disease transmission models presented in this chapter demonstrate the ease with which transmission occurs in the chimpanzee community in comparison to the orangutan population. This indicates that social information too is likely to flow faster and to a greater number of individuals among the chimpanzees than the orangutans,

which has clear implications for our understanding of traditions in these species. Chimpanzees and orangutans have been shown to exhibit a range of behaviours such as using tools to obtain insects or using leaves to collect drinking water that could be classed as traditions or even culture (Whiten et al. 1999, van Schaik et al. 2009b). Geographical variation in these behaviours cannot be explained by genetic or ecological differences alone and has therefore been attributed to local innovations and social learning (van Schaik et al. 2003, Whiten and van Schaik 2007, Krützen et al. 2011). Chimpanzees exhibit a greater number of cultural behaviours than orangutans, and it has been suggested that this may result from greater opportunities for social learning as a consequence of higher overall gregariousness (Whiten and van Schaik 2007). Although the spread of cultural behaviours will differ from that of disease in that individuals are unlikely to forget a learned behaviour (i.e. recover), even at very low recovery rates (which would indicate a very high probability of retaining a behaviour) disease struggled to spread between orangutans. This implies that there are also limited opportunities for the transmission of social information between orangutans which may help to explain why orangutan populations are characterised by fewer traditions.

Variation in gregariousness and consequently in opportunities for the transmission of social information has been suggested as an explanation for differences in cultural behaviours between orangutan sexes and subspecies. At Suaq Balimbing, for example, the more social females have been found to perform tree-hole tool use (using tools to obtain insects or their products from tree-holes) more often than the less social females (Whiten and van Schaik 2007). This difference in frequency may result from the less social orangutans having spent less time accompanying extractive foragers, meaning that they are less able to identify suitable opportunities to perform this behaviour

(Whiten and van Schaik 2007). Similarly, Sumatran orangutans at Suaq Balimbing have been shown to use tools to extract seeds from *Neesia* fruits while the less social Bornean orangutans at Gunung Palung do not (van Schaik and Knott 2001). These differences may result from the less social orangutans experiencing fewer opportunities to learn when and how to perform these behaviours, meaning that innovations cannot spread and eventually become extinct (van Schaik and Knott 2001, Whiten and van Schaik 2007). Overall, Bornean orangutans have been shown to be less social than those in Sumatra (Courtenay et al. 1988, van Schaik 1999) and so it would be interesting to model the spread of disease/information on a network from a Sumatran population to determine if the structure of these networks does indeed facilitate more rapid and extensive transmission.

5.5 Conclusion

The structure of the orangutan association network, combined with the generally weak relationships, appears to provide a strong resilience against diseases varying in infectiousness. In contrast, the chimpanzee network was found to be highly susceptible to infectious disease, even to diseases with very low transmission potential and rapid recovery. This was found to be the case using both the static and the dynamic model, providing confidence in this finding. Central individuals in both networks were both more likely to become infected and more likely to infect others, and the targeted vaccination of these central animals was more effective in reducing disease spread than random vaccinations. However, disease spread was so low in orangutans that vaccinations were not predicted to be effective, while in chimpanzees even relatively widespread vaccination did not prevent the occurrence of epidemics. The conservation

of chimpanzees, particularly at sites with intense human pressures and ecotourism, will be heavily dependent on the implementation and enforcement of disease prevention measures.

6. Discussion

The conservation of the great apes is at a critical point; while current pressures continue to affect surviving populations, future threats are emerging that could have potentially devastating consequences. Climate change is expected to be a major driver of biodiversity loss in the future (Thomas et al. 2004), while the rise of ecotourism will increase the risk of disease transmission from infected tourists to the apes that they are visiting (Chapman et al. 2009). In order to be able to plan for and respond effectively to these threats, it is essential to use predictive models; indeed, the use of modelling approaches to inform conservation policy is rapidly expanding (Beissinger et al. 2006, Hagerman et al. 2010). As ranges shift with the changing climate, current protected areas may not be sufficient to ensure species' survival (Heller and Zavaleta 2009). A more proactive, modelling based approach, in which species' likely responses to climatic change are incorporated into conservation planning, will be necessary. Disease outbreaks among the endangered apes need to be responded to immediately and so a predictive approach providing insights into effective disease prevention and containment is important for the success of preventative and responsive measures

employed. In this thesis, the potential effects of climate change on the survival of orangutans and that of disease transmission on both orangutans and chimpanzees were investigated using modelling approaches. The factors affecting the current distribution of the orangutan were explored, as well as the possible future impacts of climate change on their distribution. Potential vulnerability to the spread of disease and the possible use of vaccinations as a disease prevention strategy were investigated for both orangutans and chimpanzees. The results shed light on the past history of the orangutan and the evolution of sociality in great apes, and have a broad range of implications for the future survival of great ape species.

6.1 The past distribution and behaviour of the orangutan

During the early and middle Pleistocene, orangutans were distributed across much of South-east Asia (Jablonski 1998). Their subsequent range collapse has been attributed to both climatic changes and the arrival of humans (Harrison 1996, Jablonski 1998, Delgado and van Schaik 2000). In particular, increased seasonality and the emergence of the El Niño Southern Oscillation (ENSO), which are believed to have caused an increase in the unpredictability of fruiting patterns, are thought to have contributed significantly to the contraction of the orangutan range (Harrison and Chivers 2007). The time budget model (Chapter 2) showed that temperature seasonality was an important predictor of both resting time and moving time. However, increases in seasonality above the values experienced at orangutan field sites today are actually predicted to lead to decreases in both resting and moving time. It therefore seems unlikely that it was the direct effects of increases in temperature seasonality on orangutans that caused the historical range reduction. There is evidence to suggest that the increases in seasonality

were associated with an increase in grassland and a reduction in tropical forest on mainland Asia (Harrison and Chivers 2007). Thus, it seems more likely that it was this indirect effect on orangutan habitat that caused the distribution of the species to contract. The model developed here could be used in the future to assess how well estimates of the past climate predict past distributions, and to explore further if it was the loss of forest cover that caused the contraction of orangutan distribution patterns. This was beyond the scope of this thesis, but would be a useful application of the time budget model in the future.

A time budget model of the past distribution of the orangutan could also be used to investigate patterns of orangutan sociality during this period. There is considerable debate over the degree of sociality shown by the orangutan during the Pleistocene. MacKinnon (1971) suggested that orangutans were probably both more terrestrial and more social in the past, while Galdikas (1988) argued that the larger size of the Pleistocene orangutans and their probable heavy dependence on fruit would have made it very difficult for this species to ever have been able to meet nutritional requirements in larger groups. More recently, Harrison and Chivers (2007) suggested that the large sexual dimorphism present in Pleistocene orangutan fossils is indicative of a more gorilla-like social system. The time budget model could be used to investigate if orangutans could have been more social in the past, or if as Galdikas (1988) suggested, large group sizes would not have been sustainable. This could be achieved by incorporating reconstructions of the past climate and orangutan morphology into the time budget model, which would indicate whether or not maximum ecologically tolerable group sizes were larger across the past range of the orangutan, allowing them to be more social.

Assuming that Pleistocene orangutans were more social than contemporary populations, it is important to determine the factors that led to the adoption of a largely solitary social system. MacKinnon (1971) suggested that the current asocial and arboreal behaviour of orangutans was an adaptation to human pressures, forcing them to alter their behaviour to avoid overlap and thus contact with humans. In contrast, it has been argued that the increase in seasonality and the onset of ENSO forced the orangutan into a more solitary existence by increasing the length and severity of periods of very low fruit availability (Harrison and Chivers 2007). Alternatively, it is possible that the current solitary system evolved in response to disease pressures. Freeland (1983, 1976) suggested that much of primate behaviour, including patterns of social interaction, may have evolved to minimise the probability of acquiring pathogens. In a study of the Ebola virus in gorillas it was shown that individuals in groups were more susceptible than solitary males (Caillaud et al. 2006), while a meta-analysis across insects, birds and mammals found positive correlations between group size and both the intensity and prevalence of contagious parasites (Côté and Poulin 1995). In addition, comparison of the results of the orangutan and chimpanzee disease simulations in this thesis (Chapter 5) clearly demonstrated the increased risk of infectious disease spread in the more gregarious chimpanzee society. In the past, orangutans may have been more gregarious than observed today, in which case disease transmission could have been a serious threat. Thus, the solitary nature of the orangutan could be an adaptation to reduce disease spread between individuals. This sort of behavioural adaptation has been observed in little brown bats (*Myotis lucifugus*), a far higher proportion of which were found to roost individually following the appearance of the fungal disease white-nose syndrome than prior to the emergence of this disease (Langwig et al. 2012).

However, increasing distances from the equator have been associated with decreases in parasite prevalence in primates (Nunn et al. 2005) and decreases in the diversity of parasites and infectious diseases that infect humans (Guernier et al. 2004), with the greatest prevalence and diversity found in tropical regions. As the late Pleistocene was associated with the contraction of tropical conditions and an increase in seasonality (Jablonski 1998), it seems unlikely that disease pressures would have increased during this period. There is not currently any strong evidence for a major impact of humans on orangutans during the Pleistocene (Louys 2008) and so it does not seem probable that human pressures would have led to changes in sociality. The most likely explanation therefore appears to be that an increasingly harsh ecology characterised by less predictable fruiting patterns forced orangutans to adopt a more solitary life style (assuming that they were previously living in larger groups). The results of the time budget model strongly support this suggestion, as maximum ecologically tolerable group sizes were shown to be low across the entire orangutan range, indicating that it is ecological constraints that prevent higher sociality under current conditions. Furthermore, the model suggested the current orangutan distribution is restricted by an increased reliance on fallback foods, supporting the suggestion that orangutans are sensitive to changes in fruiting patterns. If incorporating past climates into the model showed that ecological constraints were more relaxed in the Pleistocene and became increasingly severe as the climate changed, this would add considerable weight to this argument.

6.2 The recent reduction in both the range and population size of the orangutan

Over the past 200 years, the range and population size of the orangutan have experienced particularly dramatic reductions. Genetic evidence suggests a recent population crash in North-eastern Borneo (Goossens et al. 2006), while encounter rates by hunting and collecting expeditions in the past have been shown to be considerably higher than those in recent field studies (Meijaard et al. 2010b). It has been suggested that this is largely attributable to anthropogenic impacts and in particular to the effects of the rampant deforestation that has occurred (Goossens et al. 2006). However, alternative hypotheses have also been suggested; for example, disease has been proposed as a potential explanation for population declines (Meijaard et al. 2010b), similar to those experienced by chimpanzees and gorillas following the emergence of the Ebola virus (Huijbregts et al. 2003, Bermejo et al. 2006). The findings presented in this thesis strongly support the argument that this recent range reduction is a consequence of human impacts rather than epidemics. The time budget model predicted that much of Borneo and Sumatra remains climatically suitable for orangutans; it was in fact the land cover and the human population density filters that classified these areas as unsuitable for orangutan habitation. The relative importance of these variables in determining orangutan distribution patterns in comparison to the other primate species that have been modelled using this approach (Dunbar 1992a, Dunbar 1996, Lehmann et al. 2008b, Lehmann and Dunbar 2009, Bettridge et al. 2010), suggests that for this species, human impacts have been disproportionately strong. Low maximum ecologically tolerable group sizes predicted across the orangutan range suggest that it is already living close to the limits of survival, indicating that even small declines in

habitat suitability could lead to extirpation. This may be why the orangutan range has been so strongly affected by humans, as even minor changes could make a habitat unsuitable; indeed, at a range of sites it has been found that the density of orangutans is considerably lower in logged or disturbed forests than primary forests (Davies 1986, van Schaik and Rao 1997, Felton et al. 2003, Morrogh-Bernard et al. 2003, Johnson et al. 2005, Husson et al. 2009).

In contrast, population reductions linked to an epidemic seem improbable as the disease transmission simulations indicated that disease is very unlikely to spread widely between orangutans based on their current social system. Although there is some evidence that group sizes may have been slightly higher in the past (Meijaard et al. 2010b), the minimal spread of disease that was predicted to occur between orangutans suggests that a significant increase in sociality would have to occur for disease to cause such large population decreases. The low maximum ecologically tolerable group sizes predicted across the orangutan range indicates that current ecology prevents higher levels of sociality and although some climate change has occurred over the past 200 years, this is not likely to have been dramatic enough to lead to a complete change in social system over such a short period of time. Overall, the results therefore provide strong support for the contention that over the last 200 years it is human pressures such as hunting and deforestation that have had the devastating effect on the distribution and population size of the orangutan.

6.3 The future of the orangutan in the wild

The future of the orangutan is likely to be heavily determined by the ability of conservation organisations and governments to prevent further deforestation and to

reduce the pressure of hunting on orangutans. Climate change is not predicted to have a strong effect in reducing the current range of the orangutan; in fact, most of its current range is likely to remain suitable in the future under current climate change scenarios (Chapter 3). In addition, the threat of disease to wild orangutans is predicted to be low, as long as current densities remain stable (Chapters 4 and 5). Consequently, the threats of climate change and disease arguably should not be at the head of the conservation agenda in relation to wild orangutans.

However, the warmer and wetter climates that are predicted to occur in the future may lead to increases in the prevalence of many diseases (Epstein 2001, Harvell et al. 2002). Nunn et al. (2005) found that for primates there is a higher diversity of vector-borne parasites in the tropics than in more temperate areas. As tropical conditions spread and intensify with climate change, this could lead to increases in both the distribution and prevalence of these species. Although the social system of the orangutan largely prevents the spread of diseases, individual orangutans are not likely to have a great resistance to disease as they are unlikely to have been exposed to many diseases over their recent evolutionary history. If the general prevalence of parasites increases considerably with the changing climate, this could pose a threat to the orangutan.

Currently, there is a strong focus within both conservation organisations and the Indonesian government on protecting orangutan habitat and halting the pet trade (Rijksen 1995, Nelleman et al. 2007, Orangutan Foundation 2013, WWF 2013). The findings presented in this thesis reinforce the value of these strategies; in particular, as the orangutan range is not predicted to shift dramatically in the future, protecting current habitat should be an effective conservation policy into the future. In terms of further

studies, it is clear that the effects of deforestation and human impacts such as hunting need to be incorporated into future models. Including these effects is difficult, as predicting the future locations and extent of deforestation involves the inclusion of a range of complex factors, such as the accessibility of the land and the price of timber (Kaimowitz and Angelsen 1998), while hunting pressures depend on a range of anthropological and economic variables such as cultural beliefs and the market for orangutan infants and meat (Rijksen and Meijaard 1999, Marshall et al. 2006). The inclusion of these variables will consequently be problematic, but will clearly be important for a more comprehensive view of the future distribution of the orangutan.

Increasing habitat fragmentation may force orangutans to live at higher densities in the remaining forest fragments. Orangutan densities at Sabangau are low relative to other populations of orangutans, particularly compared to those in Sumatra (Husson et al. 2009). The predictions obtained from an association network at Sabangau may not therefore be applicable for orangutans at other sites living at higher densities, and in particular for a future scenario in which orangutans may be forced into living in closer proximity to one another. At Suaq Balimbing in Sumatra, for example, orangutans live at a density of 7.0 individuals per km² (van Schaik 1999), which is actually greater than that found for the chimpanzees at Budongo (6.8 per km²; Newton-Fisher 2003). Although density is clearly not the same as sociality, as the orangutans at Suaq Balimbing are evidently far more solitary than the chimpanzees at Budongo (van Schaik 1999, Reynolds 2005), individuals living at these higher densities are likely to come into contact with one another much more frequently than those at Sabangau, providing additional opportunities for disease transmission. It would be useful in the future to model the spread of disease in a population of orangutans living at higher densities to

determine the extent to which predicted disease spread increases. Even if the chimpanzee simulations in this thesis are viewed as a worst case scenario in terms of a model of orangutans living at much higher densities in the future, the results still suggest that any increase in gregariousness could have important implications in terms of vulnerability to disease spread. In addition, the failure of simulated vaccinations to cause a considerable reduction in the spread of disease in both species (unless a large proportion of individuals are targeted) suggests that regardless of any changes to orangutan social behaviour, this will not be an effective preventative strategy.

6.4 The future of orangutans in rehabilitation centres

The continuous stream of orangutans entering rehabilitation centres and the unremitting decline in the size of wild populations indicates that rehabilitant individuals will play an important role in determining the future of the species. Rehabilitation centres act to raise money and awareness for the conservation of the orangutan through tourism, help to enforce laws preventing the trade in infants and act as a source of individuals to be reintroduced into the wild (Russon 2009). Rehabilitant orangutans are no longer reintroduced into areas that still contain wild populations, in order to prevent the spread of disease (Rijksen and Meijaard 1999, Russon 2009). Although the results presented here suggest that disease spread is not a major threat, orangutans may have a low resistance to disease and so it is still extremely important that this precautionary measure is adhered to. The time budget model suggests that it will not in fact be difficult to find areas that are climatically suitable for the orangutan. As long as anthropogenic impacts can be controlled, most of the rainforests of Borneo and Sumatra provide suitable habitats for orangutans. The future viability of areas outside the current

range of the orangutan was not investigated here, as a higher resolution approach would be recommended. Future studies should explore the impacts of climate change on specific areas, perhaps using regional climate models, which provide more accurate estimates of future climates over smaller areas (Mearns et al. 2003), to determine the exact suitability of specific regions for rehabilitation in the future. The general finding of the limited impact of climate change and the overall high climatic suitability of much of Borneo and Sumatra suggests, however, that climate change need not be a major decisive factor in choosing areas for reintroductions. Instead, it is critical that areas are selected where the forests can be protected from deforestation and where hunting pressures can be kept to a minimum.

It is essential that orangutans in rehabilitation centres are protected from disease. Juvenile and adult orangutans kept at rehabilitation centres, and those released back into the wild, are often provisioned at feeding platforms, leading to large and regular congregations of individuals, while infants are kept together at all times in nursery groups (Russon and Galdikas 1993, Russon et al. 2007, Kuze et al. 2008, Russon 2009). This system clearly leads to a more gregarious form of fission-fusion sociality than observed in wild orangutans. If the resulting social system is similar to that of the chimpanzee, it is likely to render these animals more vulnerable to disease transmission. Current evidence suggest that orangutans in rehabilitation centres are more vulnerable to disease than wild animals; for example, the prevalence of malaria was found to be significantly greater in captive and semi-captive orangutans at Sepilok Orangutan Rehabilitation Centre (SORC) than among wild individuals, possibly linked to a population density exceeding 100 animals per km² in the rehabilitation centre compared to around 2 per km² in the wild (Wolfe et al. 2002). There is also high infant mortality

among released animals at SORC and it has been suggested that this is linked to the increased aggregation sizes leading to more disease spread (Kuze et al. 2008). It would be important in the future to model the spread of disease through a rehabilitant population to gain a more in-depth understanding of the increased threat disease poses to these individuals. As these centres are major tourist attractions, the health of visitors also needs to be rigorously monitored. At SORC, for example, 15% of visitors admitted in questionnaires to experiencing symptoms of infection (Muehlenbein et al. 2010). Tighter regulations on the health of tourists need to be instigated and enforced to reduce the risk of disease transmission from the visitors to the rehabilitant orangutans. These orangutans are likely to play a central role in boosting wild population numbers and so it is vital that their health is properly managed.

6.5 The evolution of great ape sociality

The comparison of the association networks from orangutans and chimpanzees can provide insights into the social behaviour of their most recent common ancestor. This comparison highlighted two major structural similarities between the social systems, low clustering coefficients and disassortative relationships. Simple network analyses of gorilla relationships indicated that gorilla females have very weak ties with each other but are all connected to the silverback male, leading to an approximately star shaped core network (Maryanski 1987). If this is the case, gorilla groups are also likely to be disassortative and characterised by low levels of clustering. The similarity between the three could be interpreted as evidence that the social system of the most recent common ancestor of the great apes may have shared these features of social organisation. However, more detailed network analyses need to be performed on gorilla association

networks to add weight to this argument, as well as analyses on additional networks from chimpanzees and orangutans to determine how representative the networks considered here are of the species more generally. Social network analysis could also be used to explore the effect of ecology on sociality on by looking at association networks from orangutan, chimpanzee and gorilla sites that vary strongly in ecology, for example comparing the chimpanzee results with those from a more temporally variable environment, or the orangutan results with those from a Sumatran population where individuals are more social as a result of higher food availability. These analyses could be used to explore the level of plasticity expressed in regard to different fine-grained features of social structure, which would help to elucidate which features are constant across populations and species and are therefore more likely to have been inherited from a common ancestor as opposed to developed in response to local conditions. This would provide insights into the social system of the most recent common ancestor and ultimately on the evolution of sociality in the great apes.

Finally, the chimpanzee disease simulations provide insights into the potential trade-off between the benefits of rapid information transfer and the costs of increased disease transmission in highly gregarious fission-fusion species. The results of this thesis (Chapters 4 and 5) suggest that disease may not have been one of the most important evolutionary pressures for the chimpanzee, as a social system has evolved that is extremely vulnerable to disease spread. Fission-fusion sociality has been argued to be an adaptation to ecological constraints, allowing individuals to obtain many of the benefits of living in a large community, for example increased mating opportunities or defence of territories or feeding sites, without incurring the costs in terms of increased travel time (Chapman et al. 1995, Lehmann et al. 2007a). The simulation results

indicate that the fission-fusion sociality observed in the chimpanzee also provides benefits in terms of facilitating the spread of information between all individuals in the community. This means that individuals can quickly share information about food sources and predators as well as information about social relationships and the status of particular individuals within the group (Nicol 1995), information that could be extremely valuable to individuals in terms of both survival and reproductive success. In addition to the short-term transfer of information, rapid and extensive information flow may also facilitate the development and maintenance of tool-use and ultimately culture. Chimpanzee communities have large cultural repertoires that vary considerably between sites (Whiten et al. 1999). Many of the cultural behaviours or traditions provide direct benefits, such as the nutritional value of termite fishing or nut cracking (Boesch and Boesch 1982, Deblauwe and Janssens 2008). In fact, at Bossou tool use has been found to be vital for chimpanzee subsistence during periods of low fruit availability, when they rely on key fallback foods such as oil-palm nuts that they obtain through tool-use (Yamakoshi 1998). The ease with which information flows between chimpanzees may therefore provide a number of important benefits. It seems likely that these multiple benefits, in addition to the advantages of reduced travel time, outweighed any potential negative impacts from increased risk of infection during the evolution of the chimpanzee social system. It will be interesting to see if the additional disease pressures that have recently arisen, such as from ecotourism and the emergence of diseases such as Ebola, will shift the balance of this trade-off and lead to changes in chimpanzee sociality.

The predicted vulnerability of chimpanzees to disease also has interesting implications for the evolution of early human sociality, which has been suggested to have taken a

form of fission-fusion social structure similar to that observed in the chimpanzee (Foley and Gamble 2009). Presumably for humans as well as chimpanzees, benefits including the rapid spread of information were more influential in the evolution of sociality than the risks of disease transmission. This highlights the value of information flow and culture for both human and chimpanzee societies.

6.6 Conclusion

Overall, the results of this thesis contribute to the scientific basis of both orangutan and chimpanzee conservation, while also providing valuable insights into the relative importance of ecology, disease and information flow in driving the evolution of great ape social systems. The results highlight the clear value of modelling approaches to conservation biology; the methods employed in this thesis could be applied to a range of species to explore vulnerability to climate change and disease, two threats that are likely to become increasingly important in the future. Recent advances in computational power mean that a range of complex modelling techniques can now be performed without the need for specialist and expensive computer resources. Thus, all conservation planning for the future should incorporate an element of modelling, as this can considerably improve the ability to predict, and thus respond to, emerging threats to biodiversity.

Appendices

Appendix A: Age/sex classes of the orangutans

Name	Age/sex class
Archimedes	Unflanged male
Aya*	Female
Barita*	Female
Beethoven	Flanged male
Bengy	Adolescent male
Chopin	Adolescent female
Cleopatra	Female
Darwin	Unflanged male
Drake	Flanged male
Einstein	Unflanged male
Feb	Adolescent female
Fenser	Flanged male
Fossey	Female
Franky	Flanged male
Galileo*	Unflanged male
Golly	Adolescent male
Gracia	Female
Hades	Unflanged male
Hengky	Flanged male
Indah	Female
Indy	Adolescent female
Jupiter	Flanged male
Kandil*	Flanged male
Leonardo	Flanged male‡
Leony	Adolescent female
Marvin	Flanged male
Mozart	Flanged male‡
Newton*	Unflanged male
Nugget*	Flanged male
Oberon	Flanged male
Oscar*	Unflanged male
Peter Pan	Flanged male
Picasso 2	Unflanged male
Potret	Female
Qu	Unflanged male

Romeo	Unflanged male
Salvador	Flanged male
Shogun	Unflanged male
Teresia	Female
Titan*	Flanged male
Ulysses	Unflanged male
Viola	Female
Wallace	Flanged male
Willow	Female
Xylon*	Unflanged male
Zeus	Unflanged male

‘*’ indicates that individuals were isolates and ‘‡’ indicates that individuals were unflanged males at the start of the study period but were flanged by the end.

Appendix B: Sex classes of the chimpanzees

Individual	Sex
Anna	Female
Bwoba	Male
Beatrice	Female
Bahati	Female
Beti	Female
DG	Female
Duane	Male
Fred	Male
Frank	Male
Flora	Female
Gladys	Female
Gina	Female
Gashom	Male
Harriet	Female
Hawa	Male
Juliet	Female
Janie	Female
Janet	Female
Katia	Female
Keti	Female
Kigere	Female
Kalema	Female
Kana	Female
Kato	Male
Kutu	Female
Kwera	Female
Kewayya	Female
Kwezi	Male
Maani	Male
Mukwano	Female
Melissa	Female
Musa	Male
Nambi	Female
Nick	Male
Nora	Female

Oakland	Female
Pascal	Male
Rachel	Female
Ruhara	Female
Rose	Female
s1	Female
Sally	Female
Sabrina	Female
Sarine	Female
Simon	Male
Squibs	Male
Tanja	Female
Tinka	Male
Verena	Female
Wilma	Female
Zed	Male
Zefa	Male
Zig	Male
Zalu	Male
Zimba	Female

Appendix C: Individual binary network properties for each orangutan

	Degree centrality	Betweenness centrality	Closeness centrality	Eigenvector centrality
Archimedes	4	1.48	0.49	0.23
Beethoven	9	23.67	0.55	0.47
Bengy	8	8.55	0.55	0.37
Chopin	8	1.68	0.54	0.50
Cleopatra	21	76.95	0.71	0.87
Darwin	13	16.10	0.59	0.66
Drake	3	0.59	0.47	0.16
Einstein	5	1.25	0.49	0.30
Feb	26	145.89	0.78	1.00
Fenser	3	0.25	0.46	0.19
Fossey	1	0.00	0.39	0.06
Franky	9	17.58	0.55	0.41
Golly	4	0.00	0.50	0.28
Gracia	4	2.27	0.45	0.17
Hades	3	1.48	0.44	0.12
Hengky	9	3.27	0.55	0.50
Indah	20	79.28	0.69	0.85
Indy	16	88.82	0.63	0.64
Jupiter	8	36.91	0.55	0.42
Leonardo	6	0.54	0.50	0.41
Leony	2	0.26	0.38	0.07
Marvin	2	0.00	0.45	0.11
Mozart	7	19.63	0.52	0.34
Oberon	7	9.51	0.52	0.26
Peter Pan	4	0.59	0.49	0.23
Picasso 2	2	0.56	0.40	0.06
Potret	3	1.34	0.46	0.14
Qu	5	0.00	0.49	0.35
Romeo	13	18.53	0.61	0.64
Salvador	1	0.00	0.36	0.04
Shogun	5	2.26	0.49	0.32
Teresia	9	25.93	0.51	0.33
Ulysses	8	22.56	0.55	0.36
Viola	11	18.84	0.56	0.47

Wallace	10	9.79	0.54	0.51
Willow	6	7.61	0.51	0.25
Zeus	7	5.03	0.54	0.35

Appendix D: Individual weighted network properties for each orangutan

	Strength	Weighted betweenness centrality	Weighted closeness centrality	Weighted eigenvector centrality
Archimedes	0.0099	0	0.0050	0.0556
Beethoven	0.0993	35	0.0053	0.058
Bengy	0.1485	49	0.0062	0.2716
Chopin	0.0549	0	0.0060	0.1639
Cleopatra	0.2224	92	0.0065	0.9438
Darwin	0.1471	114	0.0063	0.3242
Drake	0.0017	0	0.0015	0.0052
Einstein	0.0713	89	0.0063	0.2772
Feb	0.2492	254	0.0065	1
Fenser	0.0103	0	0.0050	0.0547
Fossey	0.0006	0	0.0015	0.0038
Franky	0.0081	0	0.0038	0.0241
Golly	0.0591	0	0.0063	0.3413
Gracia	0.0813	8	0.0061	0.1411
Hades	0.0646	8	0.0062	0.1854
Hengky	0.0400	0	0.0052	0.084
Indah	0.1606	144	0.0064	0.684
Indy	0.2704	259	0.0065	0.9224
Jupiter	0.0144	35	0.0053	0.0614
Leonardo	0.0498	54	0.0055	0.0639
Leony	0.0505	0	0.0051	0.0193
Marvin	0.0017	0	0.0024	0.0085
Mozart	0.0220	0	0.0055	0.1185
Oberon	0.0376	0	0.0052	0.0381
Peter Pan	0.0256	0	0.0055	0.1023
Picasso 2	0.0131	0	0.0053	0.0229
Potret	0.0382	0	0.0047	0.0115
Qu	0.0419	0	0.0058	0.1732
Romeo	0.1520	76	0.0064	0.5983
Salvador	0.0001	0	0.0004	0.0001
Shogun	0.0119	35	0.0051	0.0552
Teresia	0.1226	85	0.0063	0.2342
Ulysses	0.0992	136	0.0064	0.3785

Viola	0.1658	134	0.0055	0.1227
Wallace	0.0123	0	0.0042	0.0436
Willow	0.0490	35	0.0049	0.038
Zeus	0.0413	0	0.0059	0.1944

Appendix E: Individual binary network properties for each chimpanzee

	Degree centrality	Betweenness centrality	Closeness centrality	Eigenvector centrality
Anna	47	0.56	0.89	0.90
Bwoba	45	0.27	0.86	0.86
Beatrice	47	0.67	0.89	0.90
Bahati	45	0.27	0.86	0.86
Beti	43	0.07	0.83	0.83
DG	38	0.07	0.77	0.74
Duane	42	0.10	0.82	0.81
Fred	53	2.34	0.98	0.99
Frank	53	2.34	0.98	0.99
Flora	46	0.54	0.87	0.88
Gladys	41	0.07	0.81	0.79
Gina	41	0.07	0.81	0.79
Gashom	43	0.12	0.83	0.83
Harriet	53	2.34	0.98	0.99
Hawa	54	3.56	1.00	1.00
Juliet	53	2.34	0.98	0.99
Janie	54	3.56	1.00	1.00
Janet	54	3.56	1.00	1.00
Katia	54	3.56	1.00	1.00
Keti	25	0.05	0.65	0.49
Kigere	54	3.56	1.00	1.00
Kalema	54	3.56	1.00	1.00
Kana	48	1.75	0.90	0.90
Kato	54	3.56	1.00	1.00
Kutu	54	3.56	1.00	1.00
Kwera	54	3.56	1.00	1.00
Kewayya	54	3.56	1.00	1.00
Kwezi	54	3.56	1.00	1.00
Maani	43	0.07	0.83	0.83
Mukwano	53	2.34	0.98	0.99
Melissa	53	2.34	0.98	0.99
Musa	54	3.56	1.00	1.00
Nambi	54	3.56	1.00	1.00
Nick	54	3.56	1.00	1.00

Nora	53	3.23	0.98	0.98
Oakland	42	1.05	0.82	0.80
Pascal	54	3.56	1.00	1.00
Rachel	54	3.56	1.00	1.00
Ruhara	53	2.34	0.98	0.99
Rose	53	2.34	0.98	0.99
s1	39	0.60	0.78	0.75
Sally	44	0.30	0.84	0.85
Sabrina	50	1.34	0.93	0.95
Sarine	53	2.34	0.98	0.99
Simon	53	2.34	0.98	0.99
Squibs	54	3.56	1.00	1.00
Tanja	45	0.46	0.86	0.86
Tinka	51	1.63	0.95	0.96
Verena	49	1.23	0.92	0.93
Wilma	52	2.02	0.96	0.98
Zed	54	3.56	1.00	1.00
Zefa	53	2.34	0.98	0.99
Zig	54	3.56	1.00	1.00
Zalu	54	3.56	1.00	1.00
Zimba	54	3.56	1.00	1.00

Appendix F: Individual weighted network properties for each chimpanzee

	Strength	Weighted betweenness centrality	Weighted closeness centrality	Weighted eigenvector centrality
Anna	2.3928	1	0.0079	0.1878
Bwoba	3.3398	52	0.0092	0.2766
Beatrice	0.9659	0	0.0056	0.0592
Bahati	2.7953	24	0.0101	0.2263
Beti	1.7094	0	0.0067	0.1251
DG	0.2289	0	0.0023	0.0166
Duane	1.4088	0	0.0062	0.0814
Fred	9.9034	8	0.0137	0.9634
Frank	9.6278	75	0.0136	0.9343
Flora	2.3882	38	0.0082	0.1791
Gladys	1.0968	44	0.0037	0.0273
Gina	1.0514	7	0.0036	0.0234
Gashom	1.5717	46	0.0069	0.0944
Harriet	5.6346	5	0.0120	0.5024
Hawa	10.0603	2	0.0137	0.9827
Juliet	6.1971	93	0.0125	0.5490
Janie	5.8777	2	0.0116	0.4659
Janet	5.7553	5	0.0115	0.4566
Katia	4.5271	0	0.0098	0.3434
Keti	0.2075	3	0.0054	0.0069
Kigere	2.4923	54	0.0080	0.1727
Kalema	7.1164	89	0.0128	0.6296
Kana	3.2692	77	0.0108	0.2669
Kato	9.6239	1	0.0136	0.9368
Kutu	7.3866	159	0.0134	0.6651
Kwera	7.5745	44	0.0129	0.6900
Kewayya	4.7313	8	0.0101	0.3603
Kwezi	8.2768	0	0.0131	0.7714
Maani	1.3704	0	0.0067	0.0931
Mukwano	4.9746	0	0.0113	0.4114
Melissa	4.6638	0	0.0107	0.3926
Musa	8.9989	0	0.0133	0.8721
Nambi	8.9147	0	0.0134	0.8495

Nick	9.7442	35	0.0137	0.9492
Nora	8.9620	0	0.0135	0.8475
Oakland	0.5778	2	0.0042	0.0470
Pascal	9.6831	0	0.0136	0.9399
Rachel	9.4083	15	0.0138	0.8963
Ruhara	6.8276	15	0.0127	0.5698
Rose	6.8371	31	0.0127	0.5737
s1	0.6421	0	0.0039	0.0517
Sally	0.2912	0	0.0052	0.0156
Sabrina	2.8998	109	0.0091	0.2101
Sarine	6.3308	19	0.0124	0.5437
Simon	7.8326	16	0.0131	0.7074
Squibs	9.7518	2	0.0136	0.9529
Tanja	0.7419	12	0.0046	0.0468
Tinka	5.3994	99	0.0115	0.4729
Verena	2.6732	17	0.0087	0.2067
Wilma	6.3234	10	0.0124	0.5413
Zed	9.8894	0	0.0136	0.9642
Zefa	7.9539	0	0.0128	0.7664
Zig	7.5841	2	0.0125	0.7119
Zalu	10.2361	6	0.0138	1.0000
Zimba	7.2780	42	0.0123	0.6800

Appendix G: ODD protocol for an orangutan agent based model

Model description

Purpose

The purpose of the model is to use simple behavioural rules to reproduce general patterns of orangutan sociality. The output of the model can be compared with a social network based on observed associations to confirm its validity. The spread of disease can then be simulated to determine the size of an average epidemic for diseases with different parameters. The overall aim is to compare these results to those obtained using network analysis to determine if the higher temporal resolution in agent based models leads to different patterns of disease spread.

State variables

The agents are 46 orangutans. Individuals have both an age/sex class (adolescent female, adult female, unflanged male or flanged male) and a residential status (resident, regular visitor, occasional visitor or rare visitor). The number of orangutans in each category is based on the actual Sabangau population (Table G.1).

Table G.1: Residential status of orangutans of different age/sex classes at Sabangau

	Resident	Regular	Occasional	Rare	Very Rare
Adult females	2	2	3	1	2
Adolescent females	2	0	1	1	0
Flanged males	3	4	4	2	3
Unflanged males	1	2	5	4	4

The global environment is composed of patches, each representing a square of habitat 50m by 50m. These patches are separated into those that contain potential orangutan food trees and patches that do not contain any potential food trees. In a plot at Sabangau, trees over 6cm DBH (diameter at breast height) were sampled (Morrogh-Bernard 2009). Of these, 53% were found to have a DBH between 6 and 10cm while 47% were greater than 10cm. As orangutans almost always feed in trees measuring > 10cm DBH, these were classed as orangutan feeding trees (Morrogh-Bernard 2009). The agent based model runs at a patch level rather than a tree level, and so 47% of patches are set as containing potential feeding trees. This is evidently a simplification as it assumes patches are homogenous – a patch is either made up solely of trees measuring less than 10cm DBH, or only those measuring greater than 10cm DBH and less than 6cm DBH. However, the habitat at Sabangau is an irregular mosaic of primary forest and areas that have been logged at various times in the past. Much of the study area is in fact covered by forest with low densities of larger trees, and so splitting the patches in this way should capture some of this irregular forest structure.

At Sabangau the percentage of orangutan feeding trees in fruit varies from around 2-9% per month, those in leaf from 20-50% and those in flower from 2-11% (Morrogh-Bernard 2009). A percentage is chosen from within these ranges and the equivalent number of patches set as in fruit, flower or leaf. This is a simplification as it assumes that all trees in the area are producing food at the same time, which may lead to unrealistically few patches of resources. However, orangutans in fact spend most of their feeding time on trees greater than 20cm DBH, which make up only 9.5% of all trees over 6cm DBH, meaning that orangutan resources are in fact spatially patchy. In addition, the validity of these assumptions can be tested by comparing the output of the

model with observed data from Sabangau, for example comparing the daily distance travelled and the percentage of time spent eating fruit, flowers and leaves predicted by the model with those observed in reality. If the model adequately reproduces the patterns found in reality, these assumptions can be justified; however, if the model produces very different patterns, the model parameters need to be adjusted to represent more closely orangutan behaviour.

Fruiting, flowering and leafing patches are all given an energetic content; fruit patches are randomly allocated an energy level between 800 and 3600, flowering patches between 200 and 800 and leafing patches between 150 and 200. These values are in proportion to the percentage of time that orangutans at Sabangau spend eating these three types of food. When an orangutan feeds, the patch loses 150 in energy. At Tanjung Puting it was shown that most feeding bouts lasted between 10 and 19 minutes, and 60% of feeding bouts on leaves lasted less than 10 minutes (Galdikas 1988). Orangutans clearly move regularly between feeding bouts and in particular are unlikely to remain on a leafing patch for more than one time step (30 minutes). A patch therefore lose 150 energy per time step that an orangutan feeds on it, so that orangutans do not feed on leafing patches for more than one time step.

Each individual has a range over which they can travel based on the actual size of home ranges at Sabangau. These territories are circles with a radius of 20 patches (each patch = 0.25 hectares) for flanged males, 18 for unflanged males and 17 for females, corresponding to areas of 314 hectares, 254 hectares and 227 hectares respectively. At Sabangau flanged male ranges average 326 hectares, unflanged males 251 hectares and females 232 hectares (Morrogh-Bernard 2009). Each patch represents 50m as this is the

distance used to calculate if orangutans are associating (Morrogh-Bernard 2009). Thus, if two individuals are within a radius of one patch they are said to be associating. The locations of the orangutans are determined by their residential status. Residents are assumed to have almost their entire home range within the global environment and are therefore placed near the centre. At Sabangau, females have been shown to form a petal distribution, with one female at the centre and other females radiating out from this (Morrogh-Bernard 2009). This is reproduced in the model. Increasingly rare visitors are placed further and further from the centre in a circular pattern, to mimic the fact that rarer animals are likely to have large parts of their home range outside of the study area (Figure G.1).

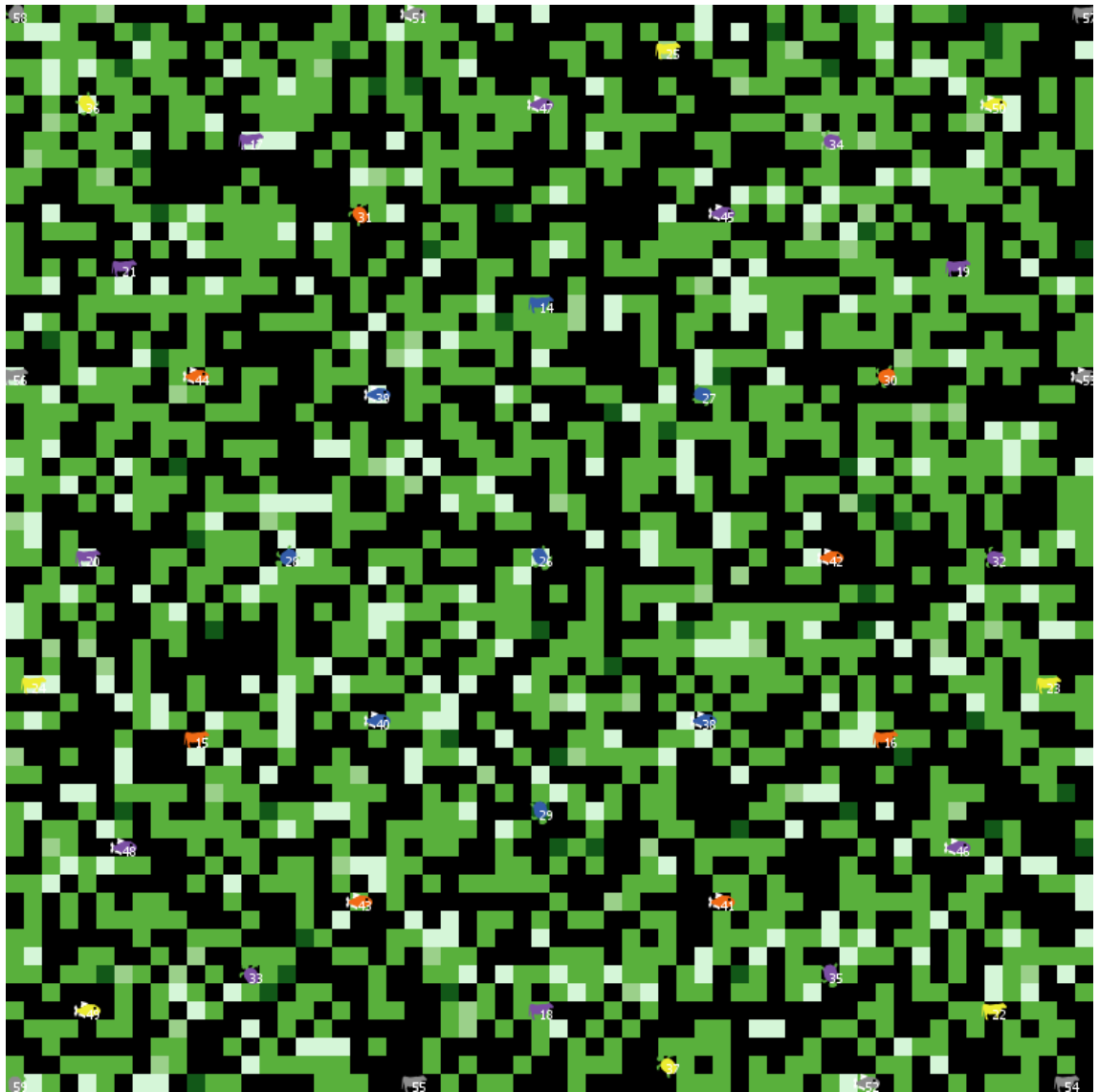


Figure G.1: The initial set-up of the agent based model. Black patches represent trees that do not provide food for the orangutans, lime green patches are trees that are not currently in fruit/flower/leaf, dark green are fruiting trees, pale green are flowering trees and white are leafing trees. Female orangutans are represented by turtles, flanged males by fish and unflanged males by cows. Blue individuals are residents, orange are regular visitors, purple are occasional visitors, yellow are rare visitors and grey are very rare visitors.

Process, overview and scheduling

The first process is to update the global environment. Food availability varies across the year at Sabangau. The percentage of trees in fruit, flower or leaf in the model is based on the range of monthly values from observed data (Morrogh-Bernard 2009). In the model, these percentages change each month, to simulate monthly variability in the number of productive trees. There are 24 time steps in a day, each time step corresponding to half an hour of the day (as the orangutans are only awake for around 12 hours a day). After 720 time steps (corresponding to a month - 30 days), new percentages for the number of patches in fruit/flower/leaf are selected from within the ranges specified above. The patches are then updated. If the new percentage for patches in fruit, for example, is higher than that in the previous month, additional patches come into fruit, if it is lower, patches are set back to normal (the selection of patches is random). This simulates seasonal changes in the availability of food as well as temporal variability in the location of food. Every two days, if the available resources on a patch have been depleted to below a resource-specific value, but it remains in fruit, flower or leaf, it regenerates and is allocated a new value for tree-energy, between its current value and the resource-specific maximum. This simulates the continuous growth of resources during the fruiting, flowering or leafing period. For leaves and flowers, the limit at which the patches regenerate is set at the minimum value of energy that they can be allocated (i.e. for leaves 150 and for flowers 200). The minimum value of energy on a fruiting patch is very high relative to leaves and flowers and so regenerating every two days would lead to high quantities of fruit all the time – at some point fruiting resources must fall below flowers or agents will only eat fruit. The value for fruit is therefore set at 250, so that the difference between the three is equivalent (i.e. 150, 200 and 250).

The orangutans are all classed as residential, regular, occasional, rare and very rare visitors. At Sabangau, residents are classed as those present during 50-100% of the months sampled, regular visitors 25-50% of months, occasional visitors 4-25% and rare visitors less than 4% of months (Morrogh-Bernard 2009). In the model, residents are therefore assumed to have a probability of being present of 0.75, regular visitors 0.38, occasional visitors 0.15 and rare and very rare visitors 0.04. Very rare individuals are rare individuals who were never observed to associate with other orangutans. These individuals have the same probability of appearing each month; however, they were observed for less time and so are included as a separate category. Each month, each agent either remains or disappears for the next month with probabilities equal to that determined by its residential class.

Females also each have a receptive status. Each female has a counter for the time in their non-receptive cycle and the time that they are receptive. Female orangutans have an interbirth interval of seven years on average in Borneo, of which they are receptive for an average of six months (Knott et al. 2009). In the model, each female starts at a random place in their non-receptive cycle. Updating females adds one to each of these counters at each time step. When they reach the end of the six and a half years they become receptive and turn white and when they then reach the end of the six months they go back to their original colour.

At each time step each individual moves according to rules associated with their age-sex class. Individuals move 50m at each time step (i.e. the width of one patch). Flanged males move first and it is assumed that they take into account the location of dominant flanged males when making foraging decision, as flanged males are very rarely found

together and so appear to avoid one another (Galdikas 1983, Morrogh-Bernard 2009). Each flanged male is given a rank – the more residential ones have higher status so that residents have the highest rank and rare visitors the lowest. Although at Sabangau male dominance fluctuates regularly (Morrogh-Bernard 2009), this was not incorporated into this model and so dominance rank was stable for the whole nine year period. The first thing that flanged males do before moving is to search for other flanged males in their immediate vicinity (100m). If there is a flanged male with a higher rank within 100m, the lower ranking male will move in the opposite direction. If there are no higher ranking flanged males in the immediate vicinity, flanged males then search for food. Orangutans have been shown to have spatial memory (Macdonald and Agnes 1999, Scheumann and Call 2006) and so are assumed to have a memory of their range and therefore know where the most productive trees are at any point in time within their range. They are also assumed to know the rough location of other flanged males in their territory, as a result of long calls. Flanged male orangutans have been found to emit long calls several times per day (Delgado et al. 2009), which can be heard over long distances, often up to 2km away (Galdikas 1981, Galdikas 1983). It has been suggested that these calls function to maintain dominance relationships and distance between males as well as to allow sexually active females to locate males (Galdikas 1983, Delgado et al. 2009). Thus, when flanged males search for food, they move towards the patch within their territory with the greatest available energy once travel costs to get there have been taken into account (i.e. energy – distance in metres to patch), and excluding patches inhabited by superior flanged males. If they move to a patch with more food than the patch that they just left, they feed and the new patch loses 150

energy. Travel costs are included to ensure that orangutans do not move every time step, travelling large distances between patches that do not vary considerably in quality.

Once all of the flanged males have moved, females move. Receptive females and non-receptive females are assumed to have different priorities. If a female is receptive, she first searches for flanged males within her territory. Again, it is assumed that females know the location of flanged males from long calls. If there is a flanged male within the female's home range she moves towards him. If there is more than one flanged male, she moves towards the one with the highest rank as it has been shown that orangutan females prefer dominant males as mating partners (Galdikas 1981). Once a receptive female has joined a flanged male she remains with him for approximately five days (mean length of consortships at Tanjung Puting = 5.4 days (Galdikas 1981) and length of oestrous is approximately five days (Nadler 1988)). There is an element of stochasticity to the length of consortships, as if a superior flanged male enters the female's territory, she abandons her consort and move towards the higher ranking male. In addition, if her consort leaves her home range, she does not follow and so the consortship terminates. Following a five day consortship, a female resumes normal activities (searching for food) for a 23 day period. This simulates a 28 day cycle (Nadler 1988), with the five day consortship assumed to occur roughly during the period when the female is in oestrous. At the end of the 23 days, she again searches for flanged males. Females remain receptive for six months (Knott et al. 2009).

Non-receptive females follow a different moving procedure. At Sabangau it has been observed that non-receptive females often avoid flanged males (Morrogh-Bernard 2009) and so if a flanged male is on the same patch as the female and she is non-receptive, she

moves back one patch. If there are no flanged males present it is assumed that her decisions are based solely on the distribution of food. Females therefore calculate which patch within their territory has the greatest available energy once travel costs to get there have been taken into account (i.e. energy – distance in metres to patch), and excluding patches inhabited by flanged males. Females then move one step towards that patch. If they land on a patch with more food than the patch that they just left, they feed and the new patch loses 150 energy.

Unflanged males were never observed within 50m of a flanged male at Sabangau (Morrogh-Bernard 2009). The first thing unflanged males do therefore is to check for the presence of a flanged male within a radius of 100m of themselves – if one is present, they move away. If they are not forced to flee, they search for receptive females. If there is a receptive female within 100m of an unflanged male, he moves towards her and remains with her for as long as possible (i.e. until the female leaves his territory or a flanged male disrupts the consortship). If there are no receptive females, he searches for other females. Unflanged males have been shown to spend a lot of time with females at Sabangau, particularly adolescent females (Morrogh-Bernard 2009). Consequently, if a female is within 100m of an unflanged male, he approaches her and stays with her for a period of time dependent on the age of the female; unflanged males in the wild stay with adult females for up to one day and adolescent females for up to one week (Galdikas 1985a, Galdikas 1985b). In the model, if the female leaves the territory of the male, or if a flanged male joins the group, the pair split up, which means that the length of time these associations last varies considerably within the restrictions set. If unflanged males have no flanged males or females within a 100m radius, they search for food. This follows the same procedure as for females in that they seek out the patch

with the highest food content once travel costs have been taken into account, excluding those currently inhabited by a flanged male. Again, it is assumed that the locations of flanged males are known from long calls.

At the beginning of the simulation one individual is selected as patient zero. This individual is randomly selected from those that are present in the area. Disease then spreads from patient zero to individuals that it is in association with (i.e. animals within 50m) with a probability equal to the transmission coefficient. Individuals recover with a probability equal to the recovery coefficient.

Design Concepts

Basic principles – Orangutan sociality is primarily determined by the distribution and availability of food, female attraction to dominant flanged males, unflanged male attraction to females (particularly receptive ones) and a degree of avoidance of flanged males.

Emergence – A realistic social network should emerge from the individual behavioural rules imposed.

Objectives – All individuals aim to maximise time spent on the most productive patches. Females aim to consort with the highest ranking males while in oestrous and unflanged males aim to maximise time spent with females, particularly receptive females.

Sensing – Individuals know the location of the most productive trees within their range – this works on the assumption that orangutans are able to remember the status of trees

within their range. Individuals also know the location of flanged males, based on long calls.

Interaction – When orangutans are within 50m of one another they are assumed to be interacting.

Stochasticity – The percentage of trees in fruit, flower and leaf changes randomly each month. The energetic value of individual patches is random, within a set range. The length of male-female associations has a strong stochastic element, as differing territorial boundaries and the random arrival of a (dominant) flanged male can break up partnerships.

Collectives – Collectives are parties of orangutans which emerge from individual behaviour, specifically the tendency of unflanged males to seek out receptive females, of receptive females to seek out flanged males and of individuals to aggregate around productive trees.

Observation – The model was tested by simulating focal observations in the model over a nine year period and comparing the resulting network with the association network obtained after actual observations over the same length of time at Sabangau. Time spent socialising, mean group size, daily distance travelled and time spent feeding on fruit, flowers and leaves were also compared against observed data from Sabangau.

Scheduling – First, trees are updated and then the receptive status of females. Flanged males move first, followed by females and then unflanged males. Associations are extracted once all individuals have moved. Disease spreads between individuals simultaneously, so that an individual cannot become infected and infect another orangutan in the same time step.

Initialisation

The model starts with 46 orangutans. There are 77760 time steps. Each time step represents half an hour and 24 time steps makes up the orangutans' 12 hour day (sleeping is not included in the model). A month is set as 30 days for simplicity. The whole model therefore represents around nine years (if each month had 30 days – so in fact slightly less than nine years). The total area is 900 hectares, which is the size of the study area.

Model Testing

The model was tested continuously to make sure that there were not any errors in the code. This involved inspecting both patches and agents after every change made to the code to make sure they weren't producing unexpected values or behaviour. This also involved a number of behaviour space experiments.

Firstly, approximately 47% of patches were set as potential feeding patches. There is a stochastic element to this process, and so there will be some variation around the 47% value. Of these patches, between 2-9% would be fruiting, 2-11% flowering and 10-50% in leaf each month. Behaviour space was used to run the setup 1000 times and the percentage of each type of patch calculated to make sure this was producing appropriate values (Table G.2).

Table G.2: The mean and range of the percentage of patches in each class created in the model setup

Patch	Mean (%)	Range (%)
Feeding	48	45.5-49.9
Fruiting	5.7	2.0-9.0
Flowering	6.7	2.0-11.0
Leafing	30.8	10.1-49.9

Every month, the percentage of trees in fruit/flower/leaf changes slightly, within its initial parameters. The code for this was tested by running the model over the full nine years and outputting the number of trees in each category each month. As expected, every 720 time steps the number of trees in each category changed, but remained within its parameters (Table G.3).

Table G.3: The mean and range of the percentage of each patch each month

Patch	Mean (%)	Range (%)
Fruiting	5.4	2.1-8.9
Flowering	6.8	2.1-10.9
Leafing	29.8	10.1-49.6

Each individual was given a territory. To ensure that they were not leaving their home range, each individual in turn was set to leave a trail marking their movements. The model was run and the trail then examined to ensure that at no point the individual left their territory (e.g Figure G.2).

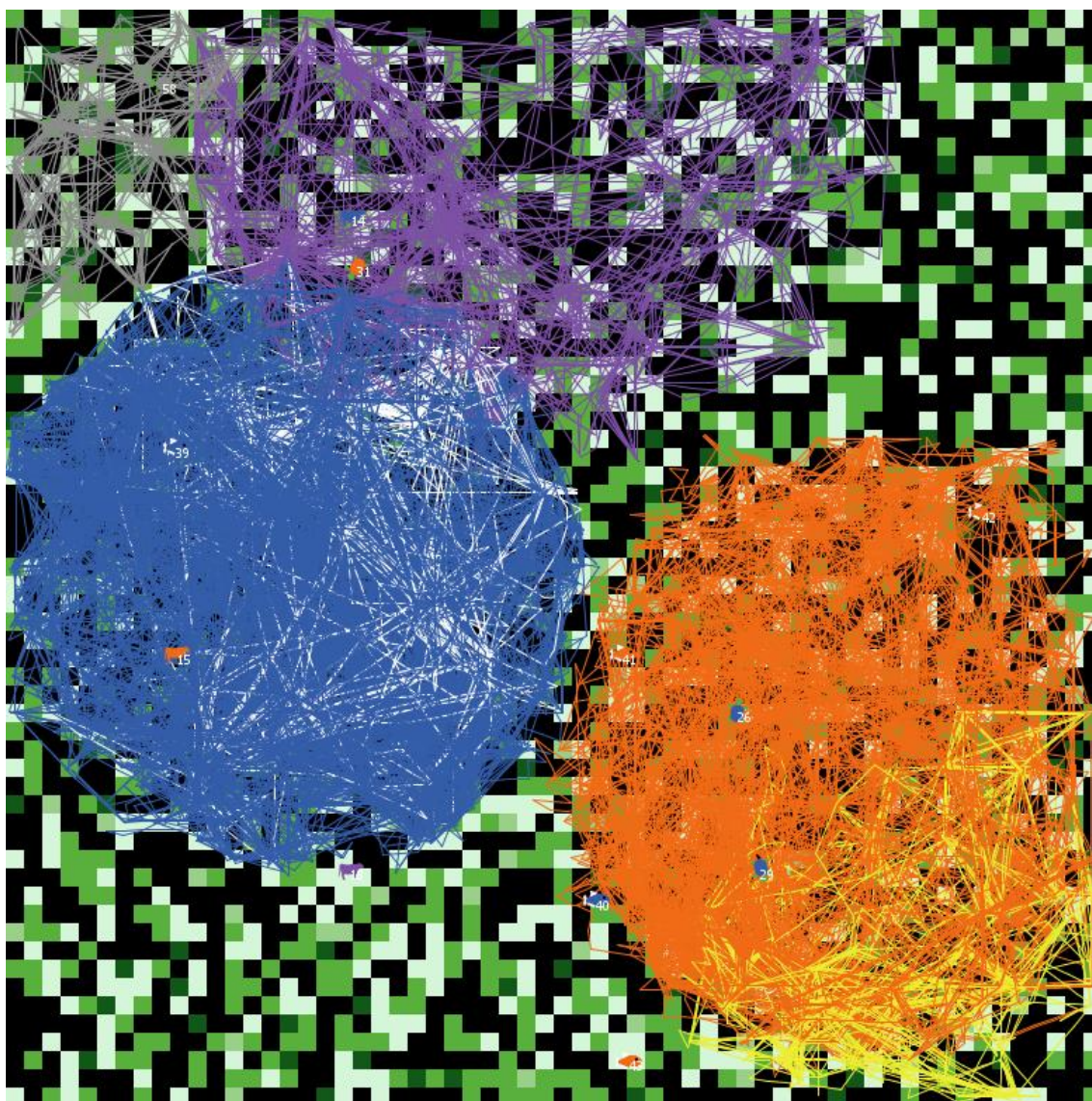


Figure G.2: Tracked movements of five individuals over the nine year simulation, demonstrating that they do not leave their home ranges.

Each individual also has a probability of being in the area, determined by their residential status. Residents are present for 75% of the time, regular visitors for 38% of the time, occasional visitors 15% and rare and very rare visitors 4%. This was tested by counting the number of individuals in each category each month over ten complete runs of the model (Table G.4).

Table G.4: Mean percentage of time each residential class spent in the area

Residential status	Mean percentage of time in area	Range
Resident	72.1	69.6-73.7
Regular	37.7	34.6-40.4
Occasional	14.6	13.4-16.0
Rare	4.3	3.7-4.7
Very rare	4.1	3.0-5.6

Flanged males are set to avoid each other. Before they move, they sense for other flanged males in a radius of two patches. If there is a dominant flanged male within this radius, they face him and move backwards one. In addition, they never move to a patch near a dominant flanged male. In theory this should mean flanged males rarely come into contact. In some cases, however, there may be three flanged males within a radius of two, and so moving away from the dominant one may mean moving closer to the subordinate one. Also, if a subordinate male is at the edge of the area, it is impossible to retreat and so he has to wait for the flanged male to leave. There will therefore be occasional flanged male contacts, but this should be rare. This was tested by calculating the number of flanged males in contact with another at every time step of the model. This number is less than 2%, which shows that flanged males are indeed avoiding each other.

Females are supposed to be unreceptive for seven years and then receptive for six months. This means that over the entire nine year period, every female should be receptive around 1.2 times. This was tested by setting a code to give a one for every female that is receptive at each time step. In total, females should be receptive for around 72,576 time steps (14 females * 4320 time steps in 6 months * 1.2). The model

was run twice and values of 86440 and 80097 were produced, close to the expected value given the stochastic nature of the model.

Comparing model output to observed data

In order to compare the model output to observed data, focal observations were simulated on the model. The number of focal observations performed on individuals over the actual study period was calculated and each individual allocated a value appropriate for its residential/age/sex class. This is their ‘focal-aim’. Between two and three times per month a present individual is selected as the focal animal. An observation time is randomly selected between one time step and 240 (equivalent to ten days), as at Sabangau focal observations lasted for up to ten days. The focal observation stops when either this time has passed or an individual’s focal-aim has been achieved. Over the nine year simulation this means that individuals are observed for an equivalent amount of time as in reality and that these observations are evenly distributed over time.

Social time – percentage of focal follow time in association

The time spent in association was very similar to the observed values (Table G.5). The observed values were calculated using focal data for only the individuals that were observed for more than 50 hours. So that the values are comparable, data were extracted from the agent based model for the individuals that were observed for more than 50 hours (i.e. data for the very rare individuals and rare females were not included). Males were slightly less social in the model than in reality, while females were slightly more social.

Table G.5: Percentage of focal follow time in association compared with percentage of time steps in association in five runs of the agent based model

	Observed (range)	ABM1	ABM2	ABM3	ABM4	ABM5	Average of the 5 ABMs
Unflanged males	27.48 (15.0-42.1)	23.08	25.27	17.18	28.98	22.45	23.39
Flanged males	3.66 (0.6-9.4)	5.08	2.84	2.30	1.95	1.38	2.71
Females	21.12 (2.7-43.5)	22.48	23.14	15.85	21.41	17.81	20.14

Mean group size

Mean group size was lower in the agent based models, but the values were still very close to reality (Table G.6).

Table G.6: Mean group size from observed data compared with that in five runs of the agent based model

	Observed	ABM1	ABM2	ABM3	ABM4	ABM5	Average of the 5 ABMs
Mean group size	1.20	1.18	1.18	1.13	1.18	1.14	1.16

Daily distance travelled

Daily distance travelled differed between the models and reality in absolute values, as unflanged males travelled less in the agent based models, while females and flanged males both travelled further (Figure G.7). However, model values are all within the range of values found at Sabangau and the relative differences were similar in the model as in reality (i.e. unflanged males generally travel the furthest, followed by females, followed by flanged males).

Table G.7: Daily distance travelled in both the observed data and five runs of the agent based model

	Observed (range)	ABM1	ABM2	ABM3	ABM4	ABM5	Average of the 5 ABMs
Unflanged males	1007 (755-1340)	823	890	838	890	873	863
Flanged males	750 (585-1098)	854	826	818	813	853	833
Females	798 (731-954)	875	848	866	862	866	863

Percentage of time spent feeding

The percentage of time spent feeding on fruit, flowers and leaves was very similar in the agent based model and reality (Table G.8). Although the values from the model are all higher, this would be expected as in the models these three food types make up 100% of feeding time, whereas in reality orangutans spend 9% of feeding time feeding on insects and bark, which were not included in the model. The relative differences between feeding times are clearly the same in the model as in reality.

Table G.8: Percentage of time spent feeding on fruits, flowers and leaves in both the observed data and five runs of the agent based model

	Observed	ABM1	ABM2	ABM3	ABM4	ABM5	Average of the 5 ABMs
Fruit	72	76.72	76.24	80.55	77.54	73.54	76.92
Flowers	15	15.84	17.51	16.12	16.09	18.29	16.77
Leaves	4	7.44	6.25	3.33	6.37	8.17	6.31

Comparing the association network from the model with that from observed data

An association network was extracted from the model. The model was run for the full 9 years and at each time step all associations recorded. This was used to create a network of dyadic association indices using the Simple Ratio Index:

$$\text{SRI} = \text{AB}/(\text{A} + \text{B} - \text{AB})$$

Where AB is the number of time steps that A and B are observed together, A is the total number of time steps in which A is observed and B is the total number of time steps in which B is observed.

The network obtained was then compared with the network based on real data to see if the model was adequately representing reality (Figure G.3). Although it is difficult to compare association networks quantitatively, if the agent based model produces a network with similar properties to the actual association network, this gives confidence in the ability of the model to represent orangutan association patterns.

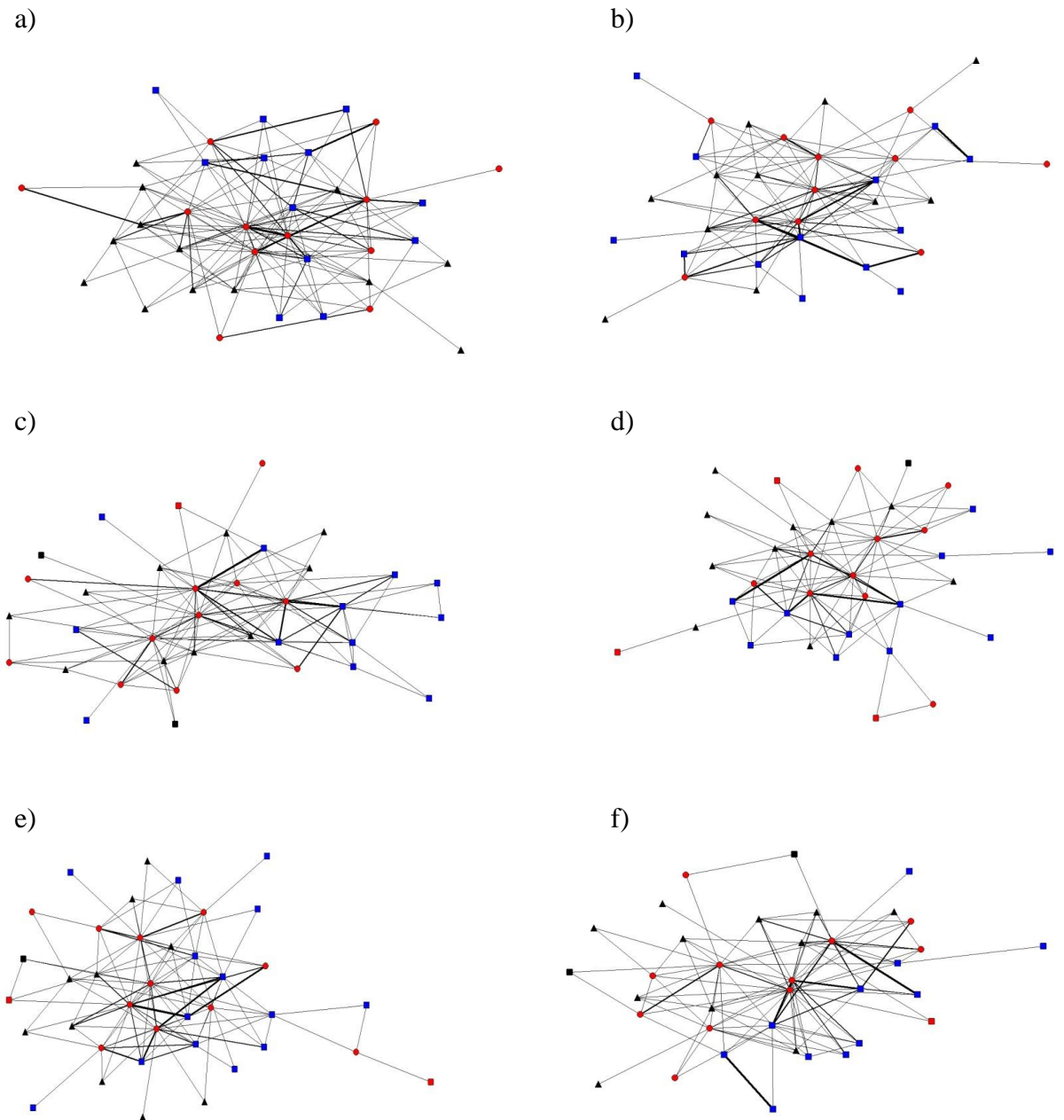


Figure G.3: Sociograms of a) the actual orangutan association network and (b-f) the association networks extracted from five runs of the agent based model

The properties of the networks were examined as further evidence of the ability of the agent based model to reproduce an association network. The networks had a number of similarities with the observed data, but also differed in a number of ways. Mean strength was higher and density and degree lower in the networks from the agent based model (Table G.9). The agent based model networks were also significantly more clustered than random while the original network was less clustered than random (Table G.9). The agent based model networks had similar path lengths to that in the association network, but were less disassortative than the association network (Table G.9). Overall, however, the results were reasonably similar.

Table G.9: Network metrics compared between the actual association network and those created from five runs of the agent based model

	Observed	ABM1	ABM2	ABM3	ABM4	ABM5	Average of 5 ABMs
Density	0.21	0.18	0.18	0.17	0.15	0.17	0.17
Mean degree	7.62	6.00	6.28	5.71	6.00	6.06	6.01
Mean strength	0.072	0.091	0.088	0.074	0.093	0.094	0.088
Clustering coefficient	0.152	0.437	0.460	0.473	0.489	0.470	0.466
Mean weighted shortest path length	7.859	4.849	8.082	7.684	7.795	12.313	8.145
Weighted assortativity coefficient	-0.248	-0.137	-0.095	0.004	-0.018	0.058	-0.038

Appendix H: The effect of centrality on both the ability to transmit disease and individual infection risk in the orangutan network

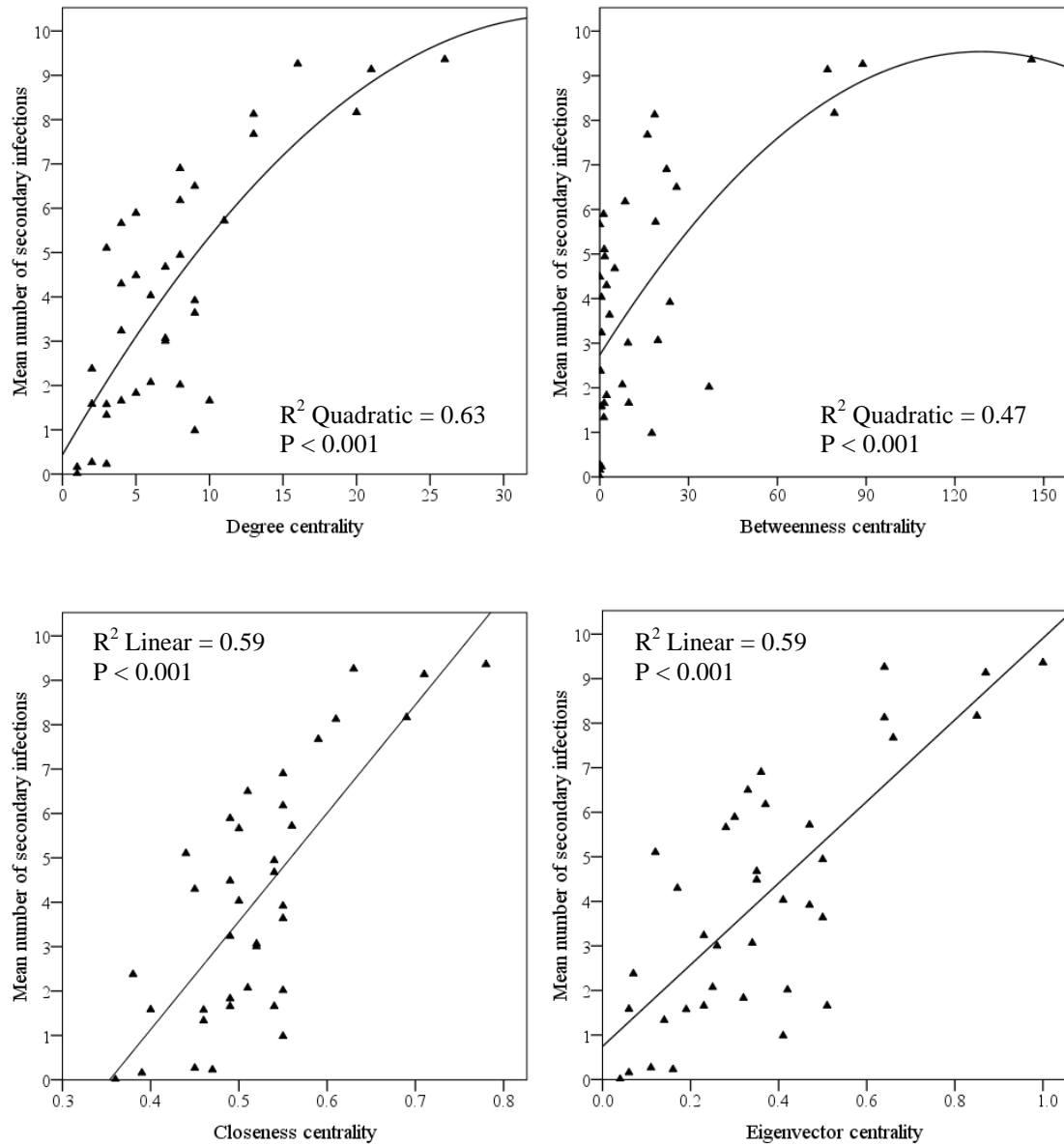


Figure H.1: Mean number of secondary cases plotted against degree, betweenness, closeness and eigenvector centrality for the orangutan network ($\beta=1.0$, $\gamma=0.1$).

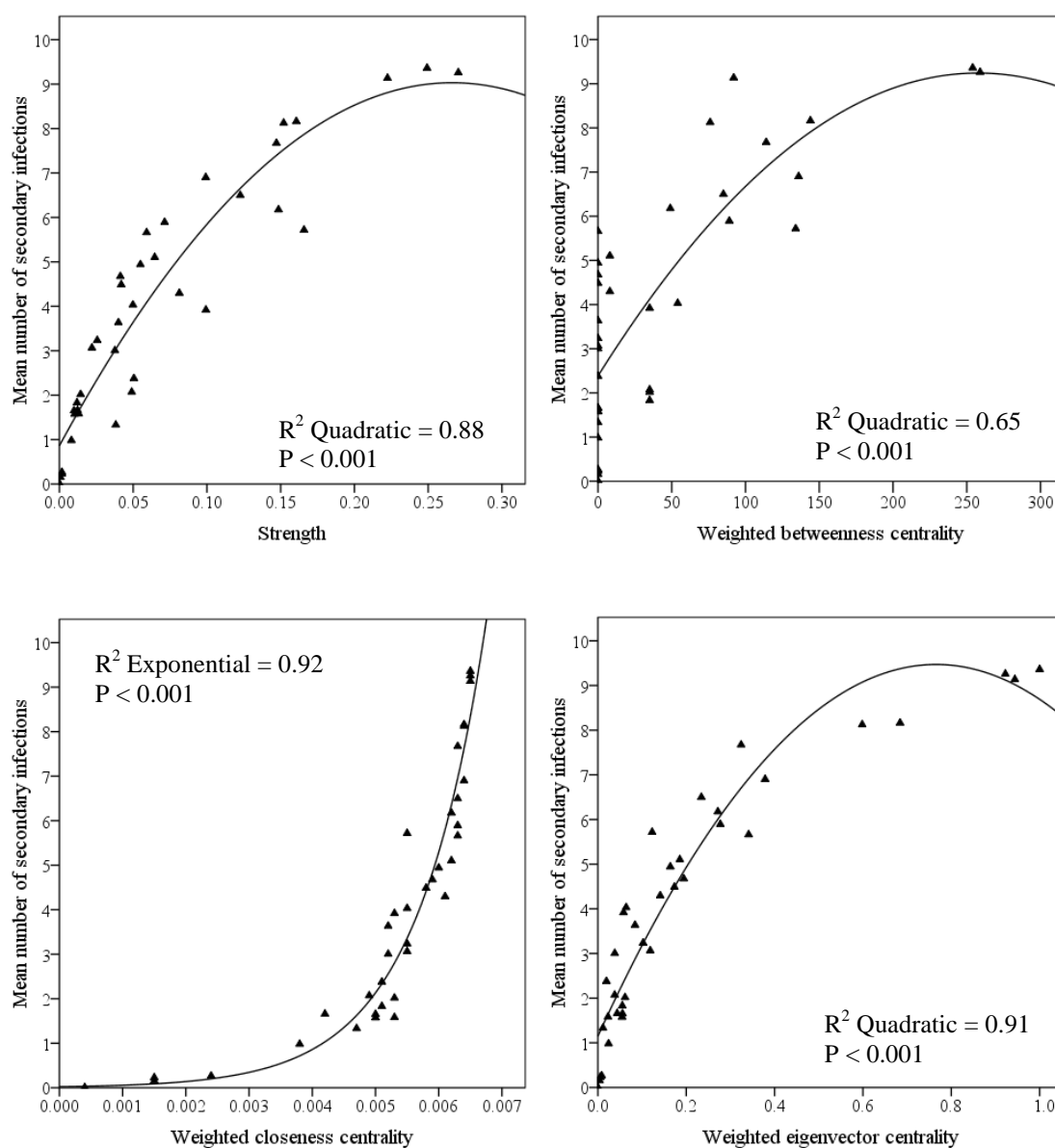


Figure H.2: Mean number of secondary cases plotted against strength, weighted betweenness, weighted closeness and weighted eigenvector centrality for the orangutan network ($\beta=1.0$, $\gamma=0.1$).

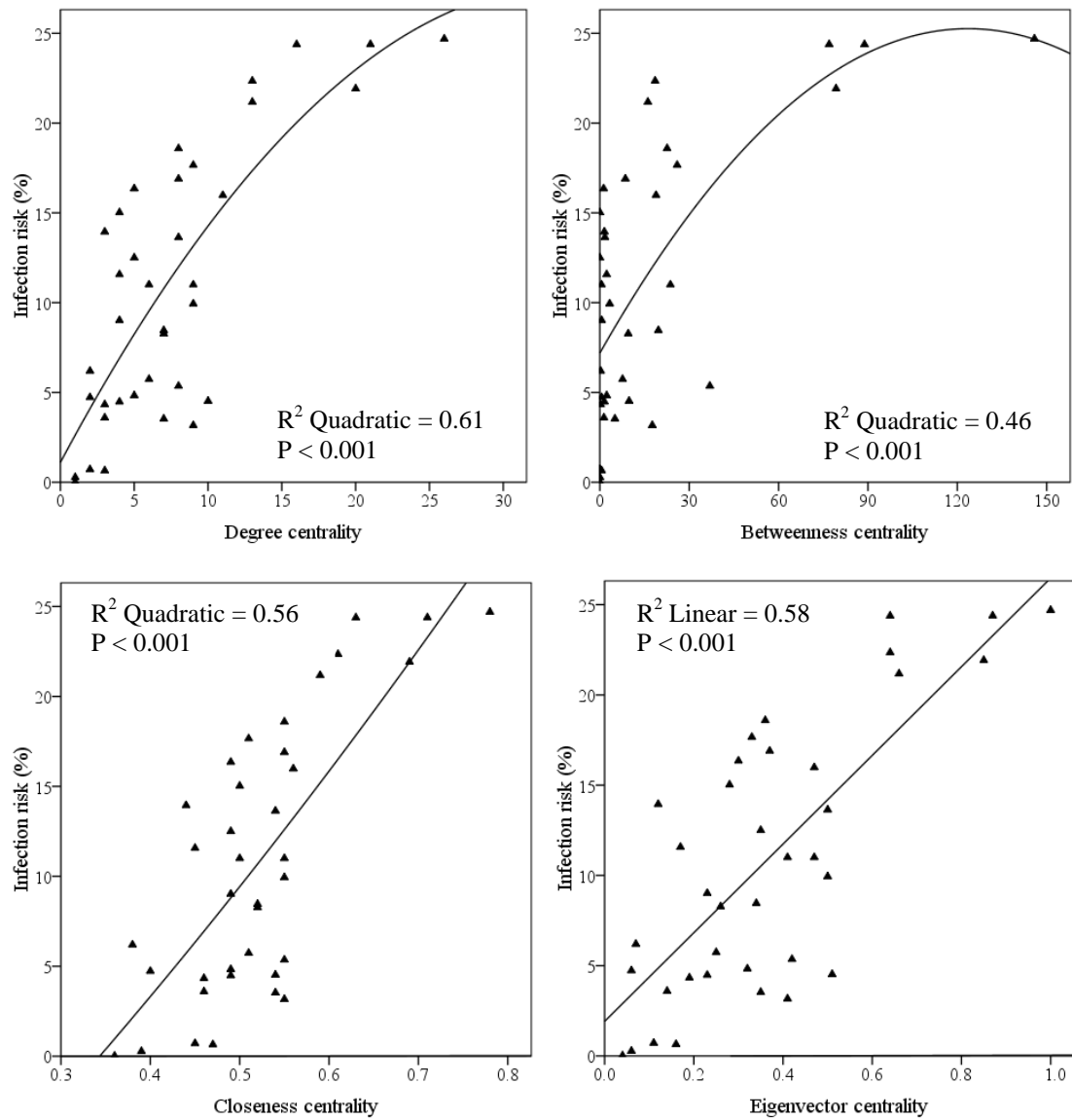


Figure H.3: Infection risk (percentage of simulations in which an individual became infected) plotted against degree, betweenness, closeness and eigenvector centrality for the orangutan network ($\beta=1.0$, $\gamma=0.1$).

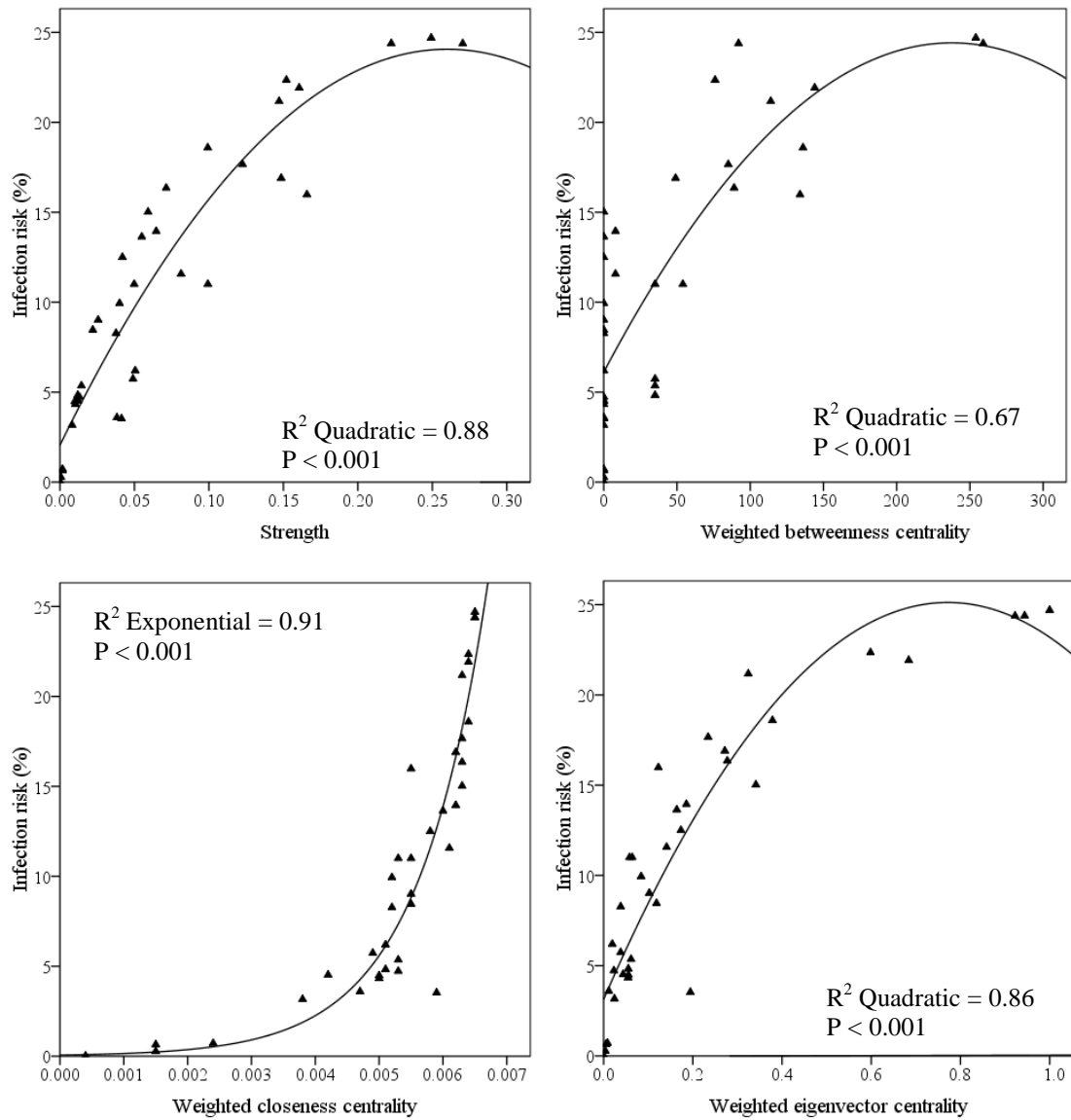
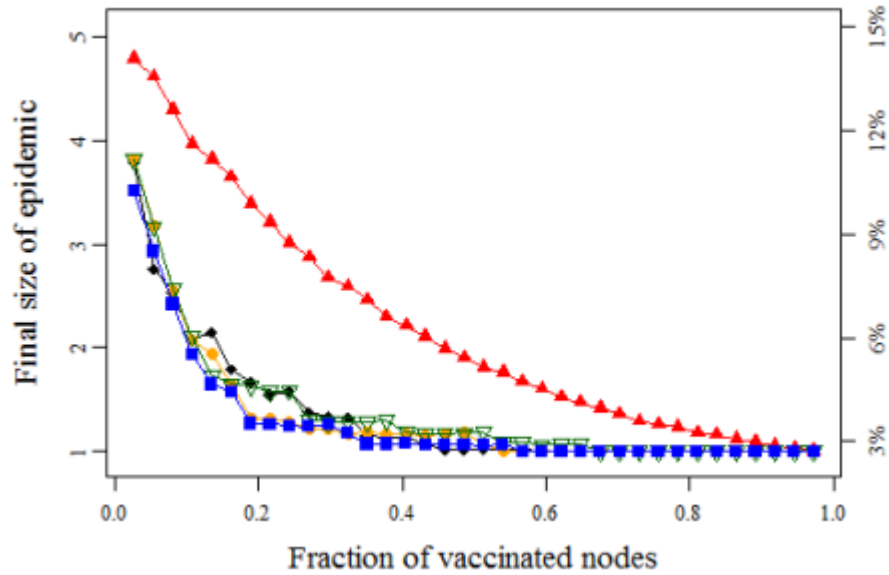


Figure H.4: Infection risk (percentage of simulations in which an individual became infected) plotted against strength, weighted betweenness, weighted closeness and weighted eigenvector centrality for the orangutan network ($\beta=1.0, \gamma=0.1$).

Appendix I: The effect of vaccination on the final size of the epidemic in the orangutan network

(a)



(b)

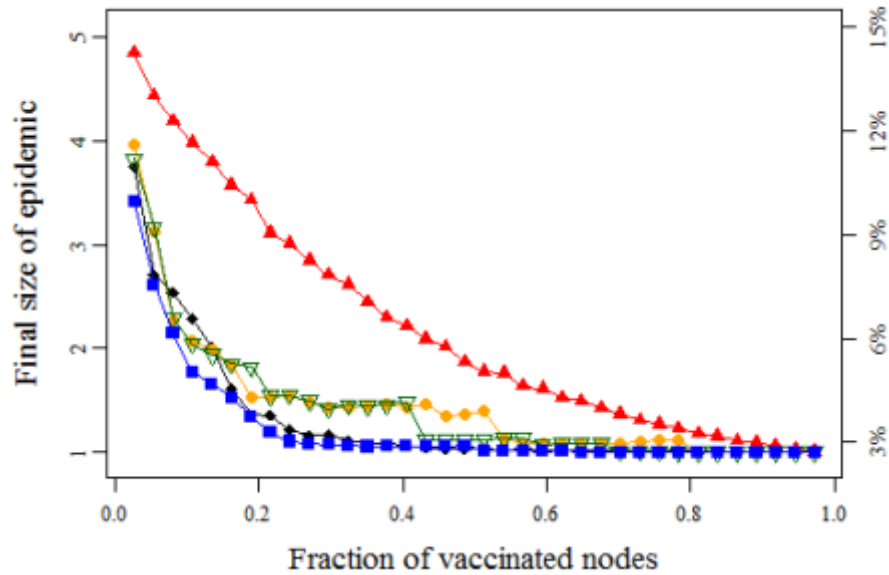


Figure I.1: The final size of the epidemic of disease with parameters $\beta=1.0$ and $\gamma=0.1$ following the vaccination of different proportions of the population. In (a) targeted vaccinations are based on binary measures of centrality, in (b) weighted measures. Red triangles indicate random vaccinations, blue squares indicate targeted vaccinations of individuals with high degree/strength, black diamonds individuals with high betweenness/weighted betweenness, yellow circles individuals with high closeness/weighted closeness and green inverted triangles individuals with high eigenvector/weighted eigenvector centrality.

Appendix J: The effect of centrality on both the ability to transmit disease and individual infection risk in the chimpanzee network

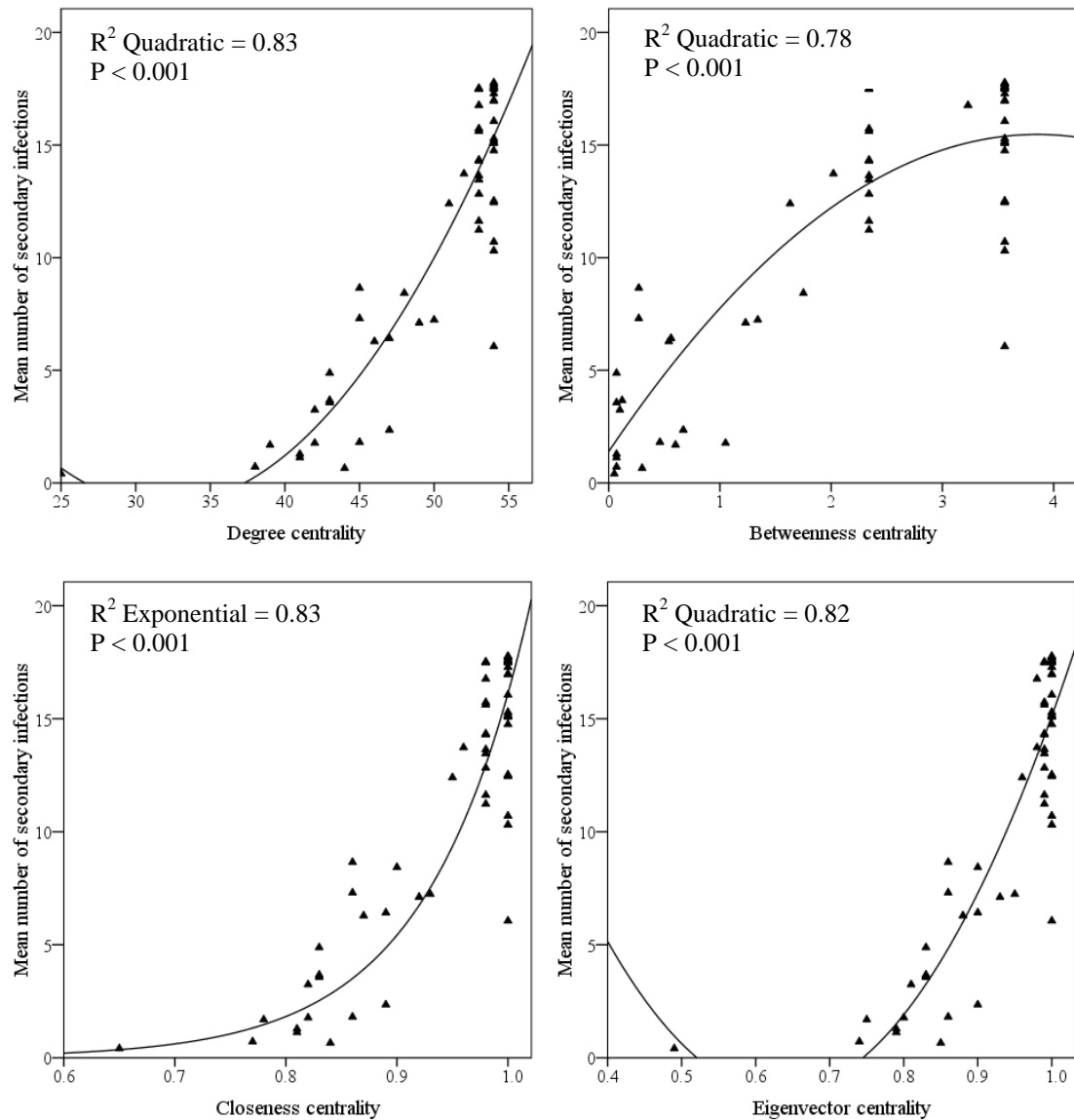


Figure J.1: Mean number of secondary infections plotted against the degree, betweenness, closeness and eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.9$.

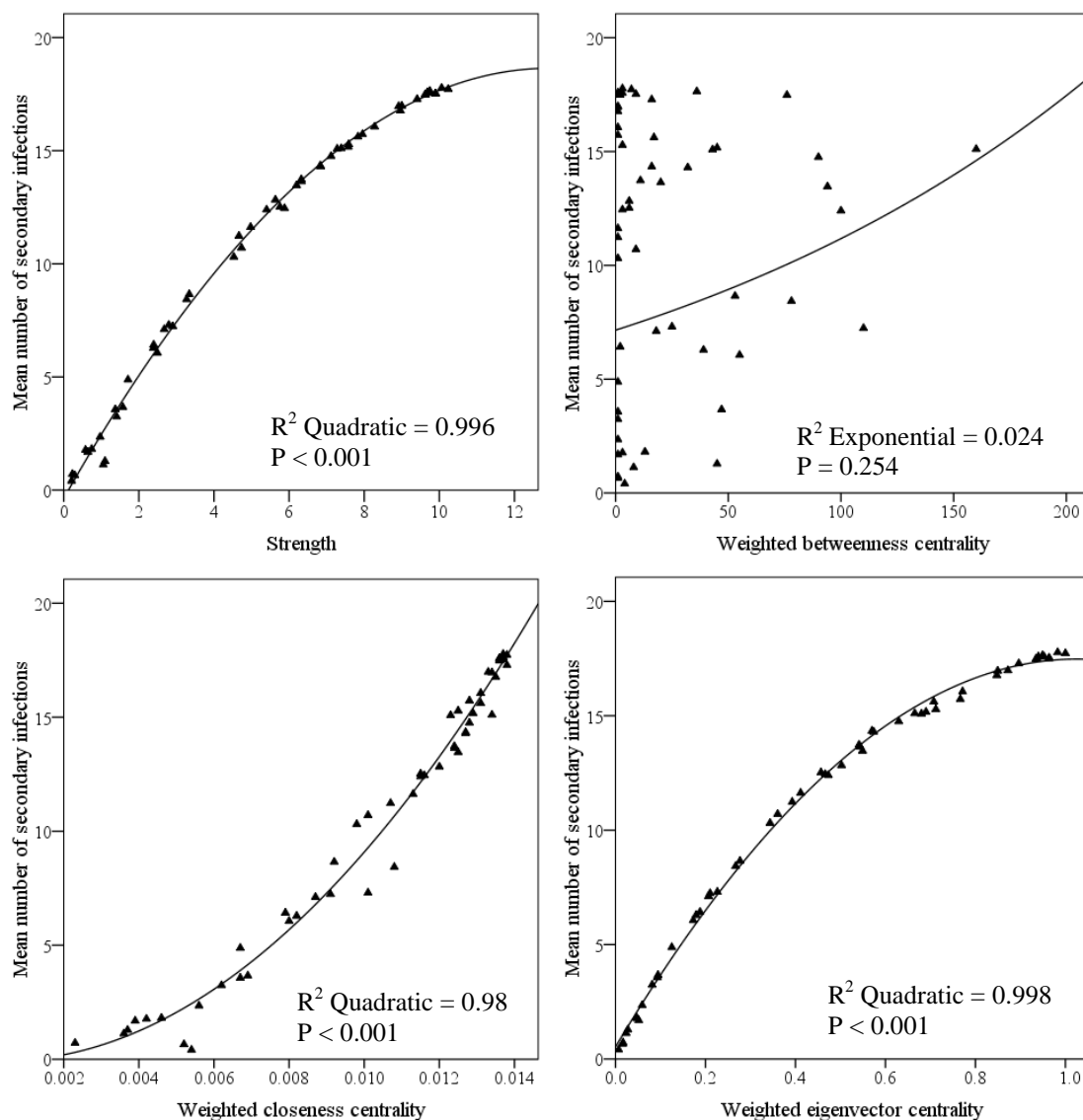


Figure J.2: Mean number of secondary infections plotted against the strength, weighted betweenness, weighted closeness and weighted eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.9$.

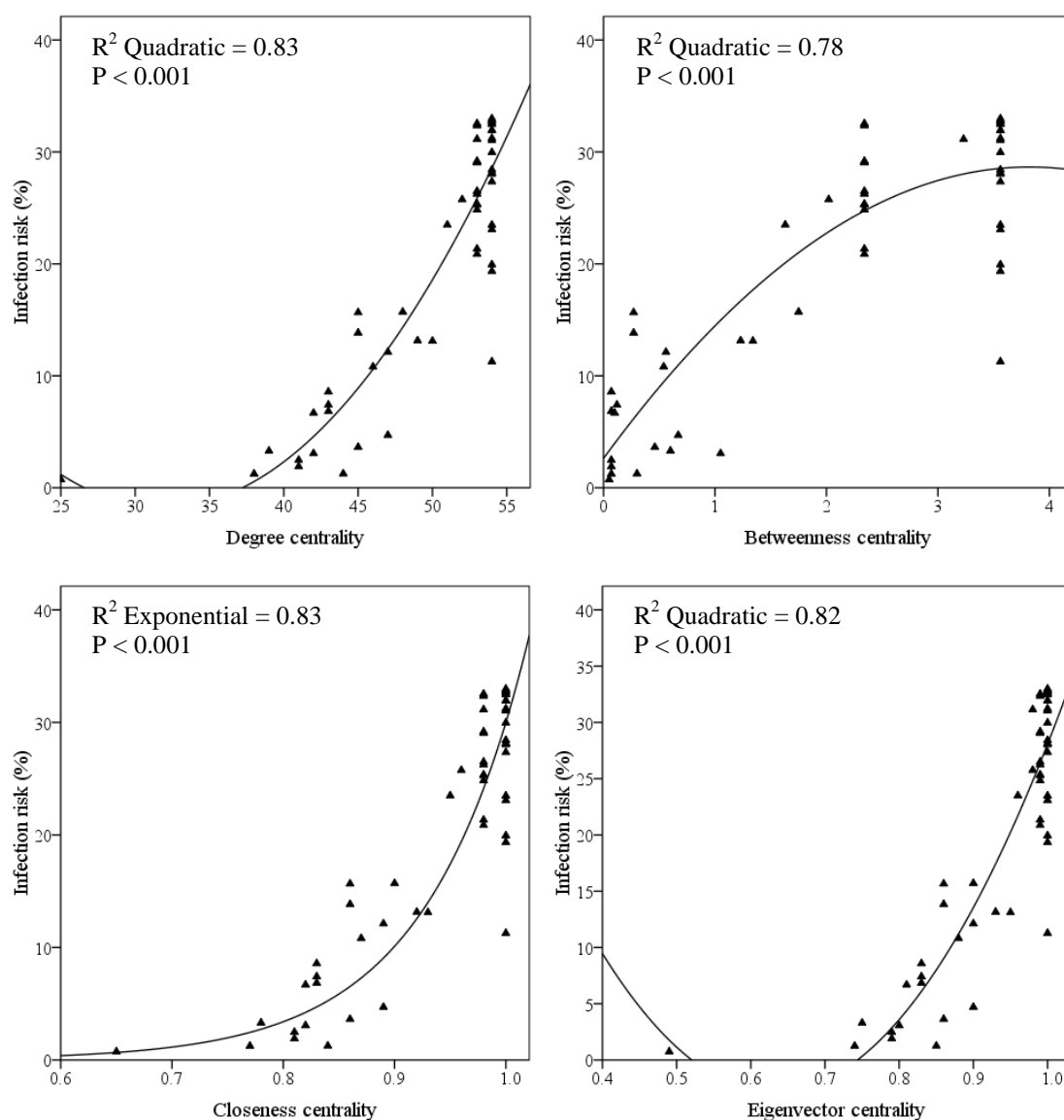


Figure J.3: Infection risk (percentage of simulations in which an individual became infected) plotted against degree, betweenness, closeness and eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.9$.

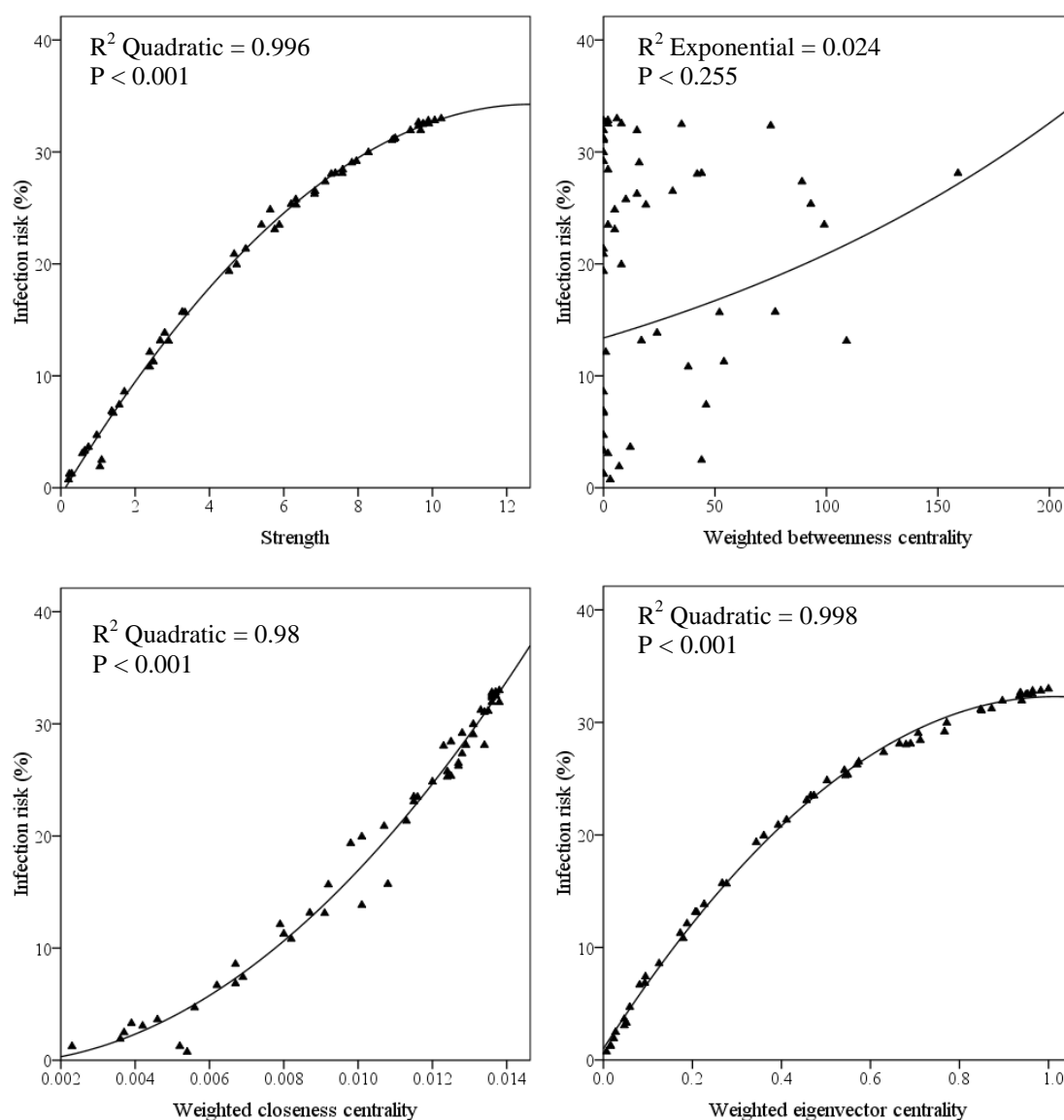


Figure J.4: Infection risk (percentage of simulations in which an individual became infected) plotted against strength, weighted betweenness, weighted closeness and weighted eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.9$.

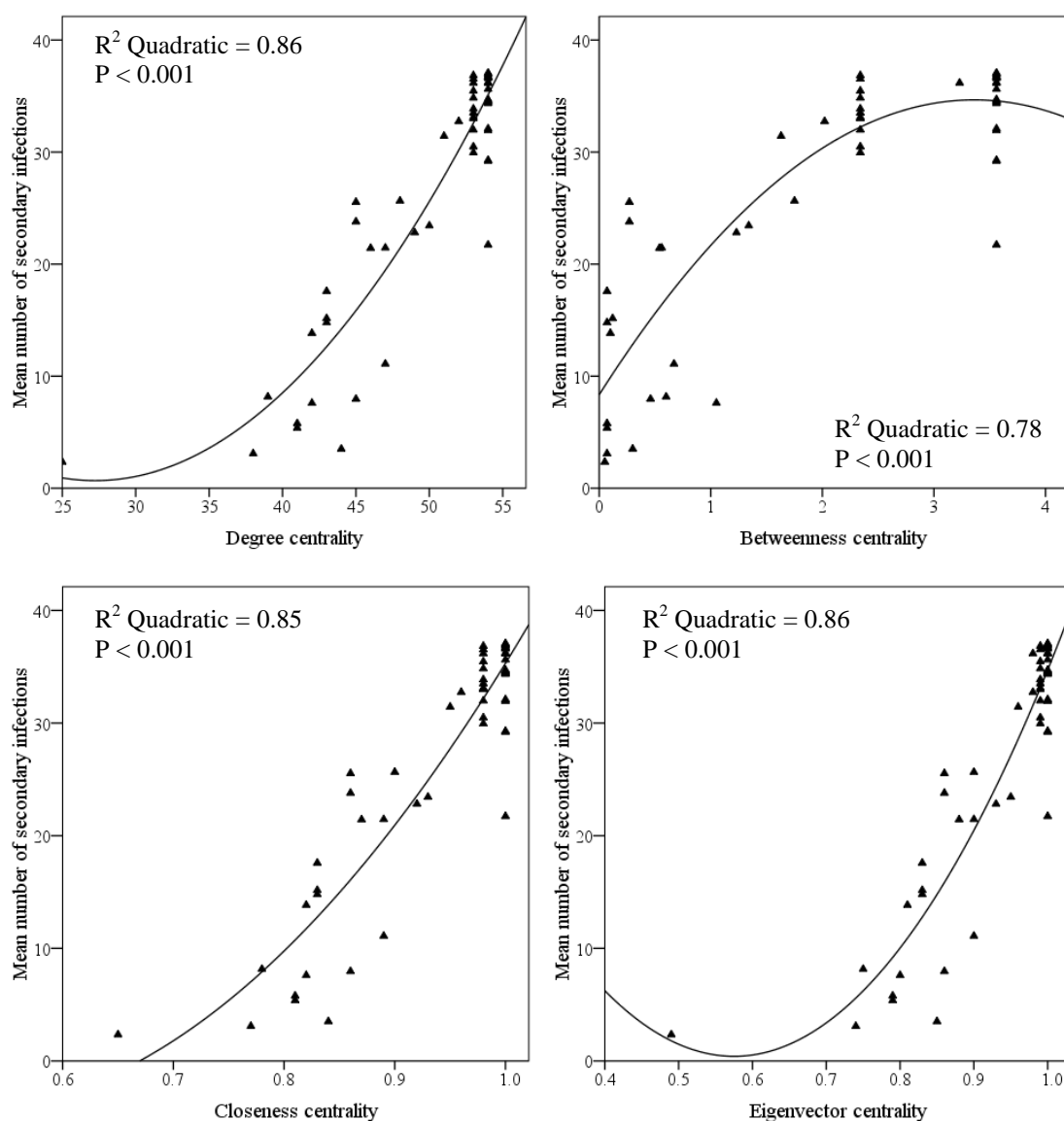


Figure J.5: Mean number of secondary infections plotted against the degree, betweenness, closeness and eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.4$.

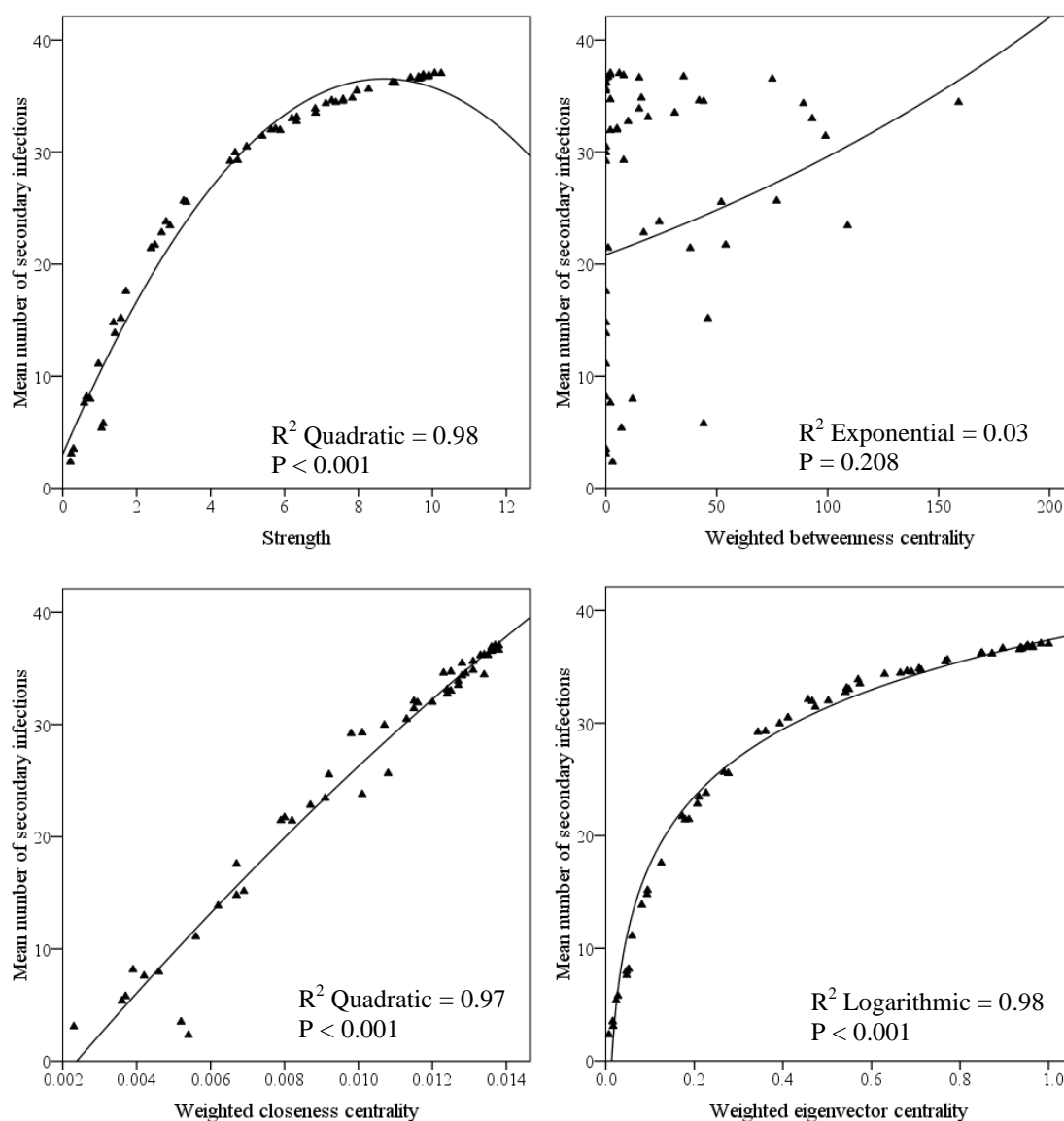


Figure J.6: Mean number of secondary infections plotted against the strength, weighted betweenness, weighted closeness and weighted eigenvector centrality of patient zero for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.4$.

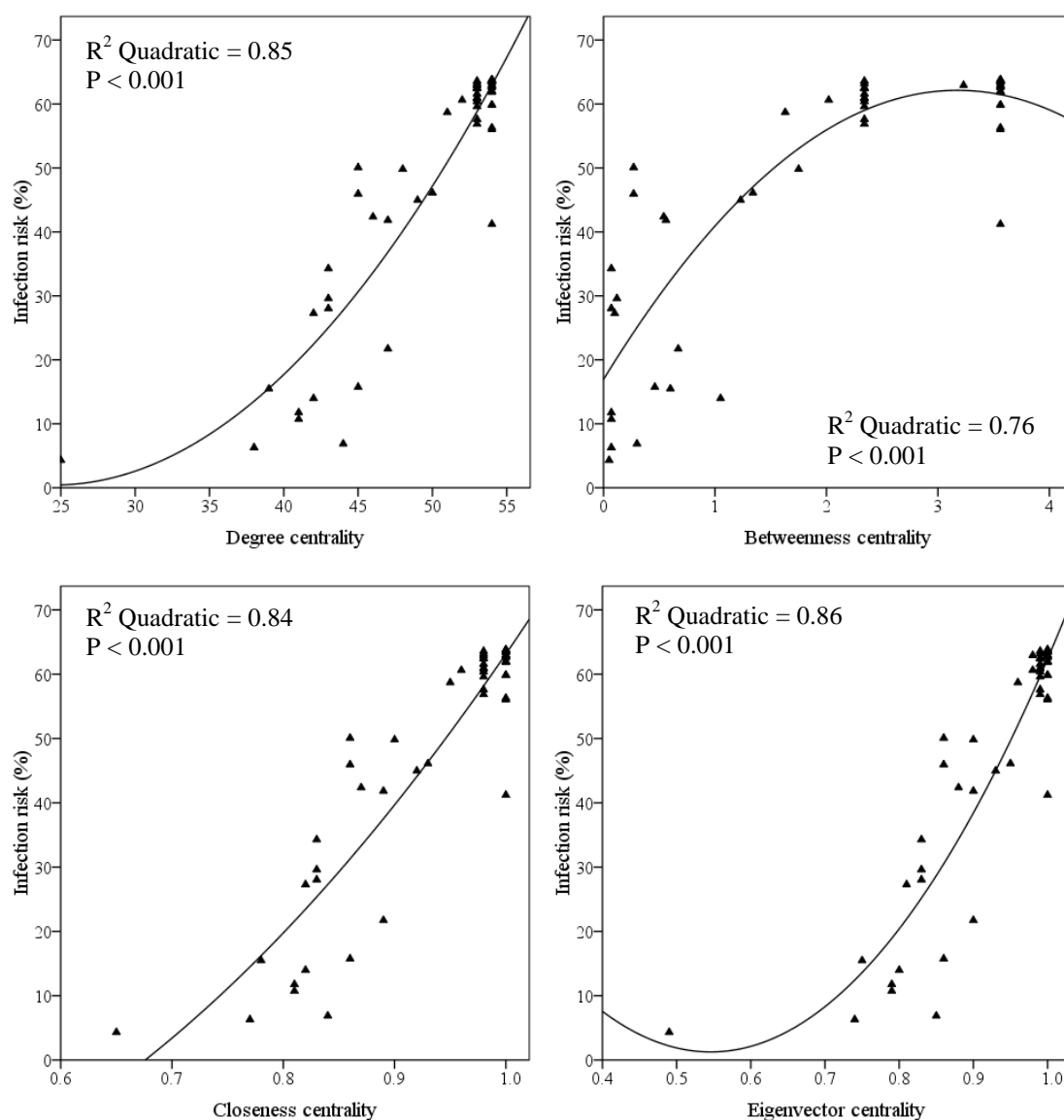


Figure J.7: Infection risk (percentage of simulations in which an individual became infected) plotted against degree, betweenness, closeness and eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.4$.

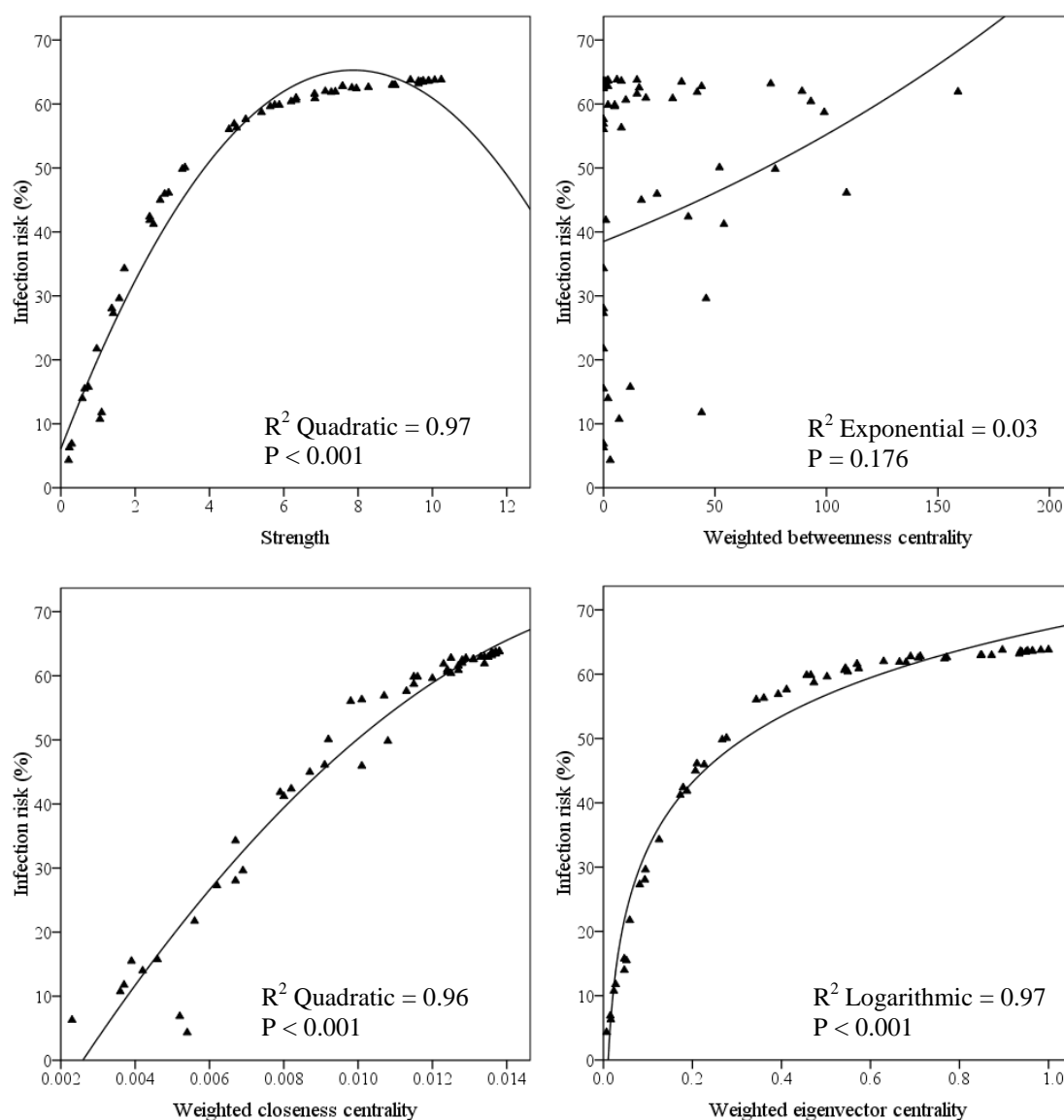
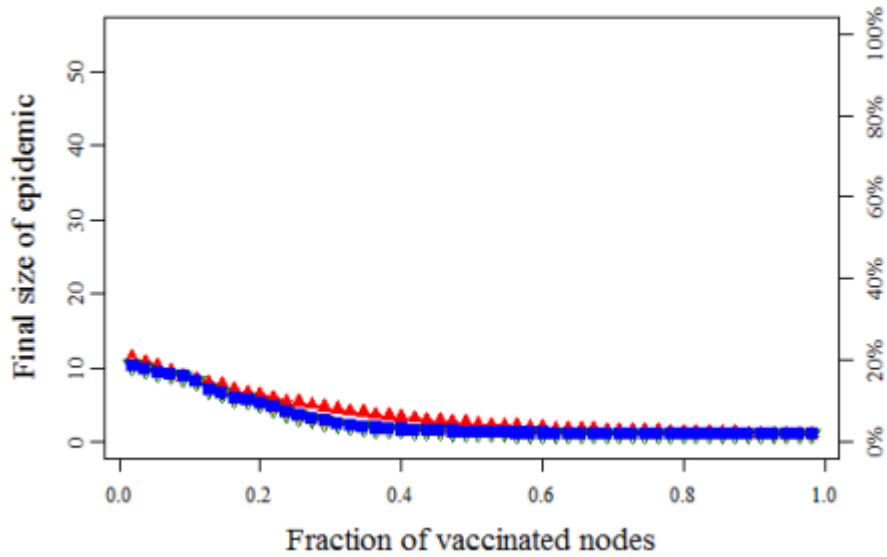


Figure J.8: Infection risk (percentage of simulations in which an individual became infected) plotted against strength, weighted betweenness, weighted closeness and weighted eigenvector centrality for the chimpanzee network for a disease with parameters $\beta=0.1$ and $\gamma=0.4$.

Appendix K: The effect of vaccination on the final size of the epidemic in the chimpanzee network

(a)



(b)

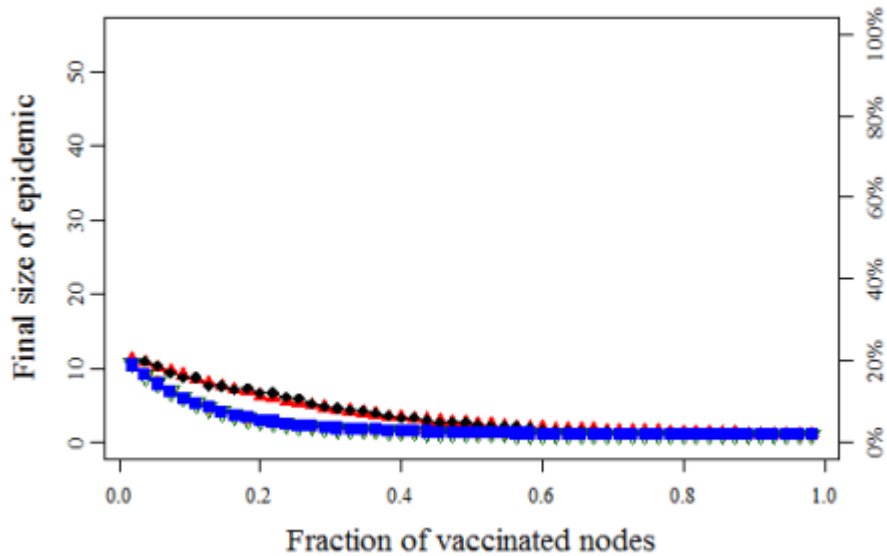
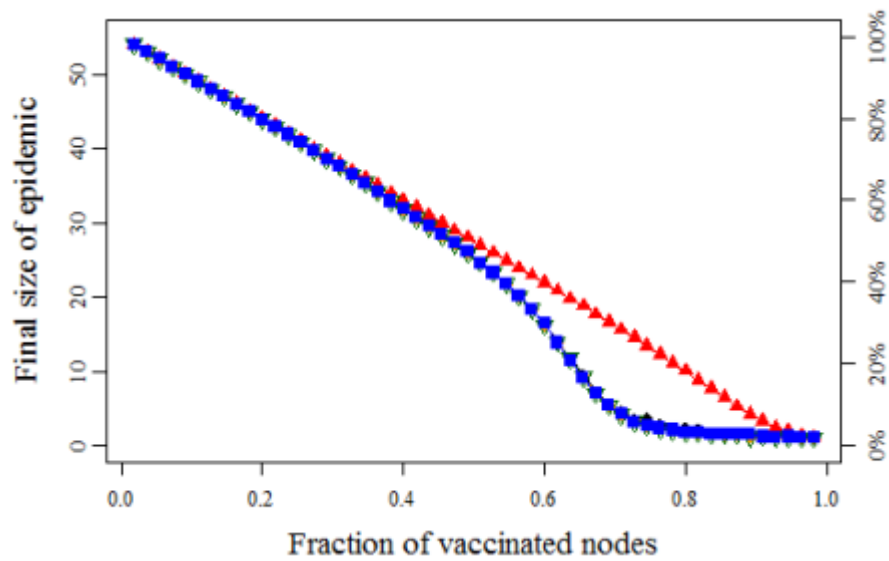


Figure K1: The final size of the epidemic with parameters $\beta=0.1$ and $\gamma=0.9$ following the vaccination of different proportions of the population. In (a) targeted vaccinations are based on binary measures of centrality, in (b) weighted measures. Red triangles indicate random vaccinations, blue squares indicate targeted vaccinations of individuals with high strength, black diamonds individuals with high weighted betweenness, yellow circles individuals with high weighted closeness and green inverted triangles individuals with high weighted eigenvector centrality.

(a)



(b)

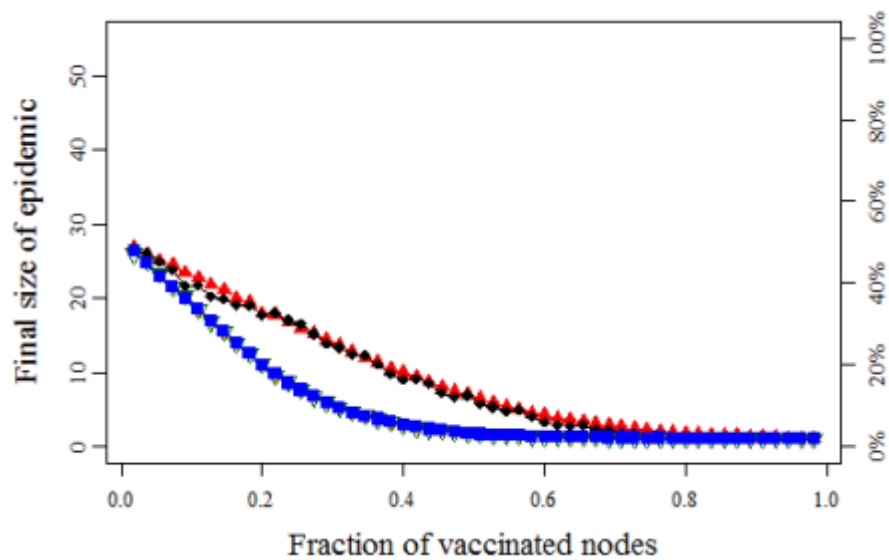


Figure K2: The final size of the epidemic of disease with parameters $\beta=0.1$ and $\gamma=0.4$ following the vaccination of different proportions of the population. In (a) targeted vaccinations are based on binary measures of centrality, in (b) weighted measures. Red triangles indicate random vaccinations, blue squares indicate targeted vaccinations of individuals with high strength, black diamonds individuals with high weighted betweenness, yellow circles individuals with high weighted closeness and green inverted triangles individuals with high weighted eigenvector centrality.

Appendix L: Comparison between the chimpanzee network based on all 30 months of data and each of the monthly networks.

Table L1: Correlations between the chimpanzee network based on all 30 months of data and each of the monthly networks. Correlations were calculated using the quadratic assignment procedure with 50,000 matrix permutations.

Month	R	P
1	0.686	<0.001
2	0.739	<0.001
3	0.651	<0.001
4	0.725	<0.001
5	0.771	<0.001
6	0.765	<0.001
7	0.713	<0.001
8	0.785	<0.001
9	0.764	<0.001
10	0.883	<0.001
11	0.862	<0.001
12	0.887	<0.001
13	0.846	<0.001
14	0.906	<0.001
15	0.864	<0.001
16	0.746	<0.001
17	0.740	<0.001
18	0.764	<0.001
19	0.894	<0.001
20	0.895	<0.001
21	0.884	<0.001
22	0.862	<0.001
23	0.794	<0.001
24	0.834	<0.001

25	0.888	<0.001
26	0.859	<0.001
27	0.779	<0.001
28	0.739	<0.001
29	0.726	<0.001
30	0.702	<0.001

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